OOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

INDO-PACIFIC FISHERIES COUNCIL

PROCEEDINGS

8th SESSION

COLOMBO

CEYLON

6 — 22 December 1958

SECTION III

SYMPOSIUM ON FISH BEHAVIOUR

Edited by G.L. Kesteven, D.Sc.

IPFC Secretariat, FAO Regional Office
for Asia and the Far East
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0. INTRODUCTION

It has long been recognized that success ɔcating and catching fish depends in large ɜure on knowledge of their individual and ctive behaviour. That behaviour charac- tics had to be known in searching for fish equally, in designing and using gear seemed ɔus, but nevertheless there did not seem to ıy particular reason to carry out systematic ırch on fish behaviour. More recently it has come to be recognized that what is thought behaviour plays an important part in those ıcteristics of a population that constitute ɔasic parameters describing its dynamics in s of numbers and biomass. This recogni- is part of a larger awareness, lately developed, need to have a more detailed account of the esses that determine growth, reproduction mortality, all of which are summarized in ɔus parameters, often on the basis of gross mptions.

It is obvious that for any species as a e and for any life-phase of it, distribution d be more effectively understood if the de- inants, internal and external to the organism, at distribution could be discovered. Such nalysis would supplement the descriptions stribution customarily prepared. The phy- gical requirements of an organism in each e of its life, and in each phase of the annual of events, must at times cause it to avoid in hostile environments and at other times ove from an indifferent environment into onments more suited to particular physiolo- conditions, if these are accessible. Its city to do these things is presumably a major of its power to survive. The analysis of the ons between behaviour and its environ- al determinants would permit development chniques of prediction of distribution from vations of environmental elements. The r understanding of distribution would make portant contribution also to understanding e basic population parameters.

These general statements must be valid for the organism with regard to its trophic, ductive and other functions, and for the unity with respect to its reproductive and ing potentials, and to its continued well- , based as these are on metabolic and osmo latory processes of its individuals.

In reality, however, researches into the behaviour of fishes have not been extensive. Although the foregoing views were held generally, there was until recently no recognition of an urgency to carry out behaviour research, for there was little optimism that concrete and practical results of direct applicability to fishery problems could be obtained. Indeed it was often thought that such work lay in the realm of purely academic research in zoology. However, this situation has changed in recent years and many fishery institutions are engaged on carefully planned research on even the most fundamental aspects of the physiological basis to behaviour. However, in many countries fishery workers have difficulty in deciding whether behaviour research should be carried out by them, and if it should, along what lines and by what methods it should be prosecuted. These questions were discussed at the Seventh Meeting of the IPFC and it was decided to make fish behaviour the subject for the Symposium at the Eighth Session.

Objectives of the Symposium

Considering the status of knowledge of behaviour of fishes and of research in this field the organisers of the Symposium held that its principal purpose should be to obtain a consensus of opinion on to questions:

(i) Why should fishery biologists investigate behaviour?

(ii) By what methods should such investigations be carried out?

The first question called for a careful scrutiny of the general propositions presented in the opening paragraphs of this introduction and for this purpose it was thought that background papers should be provided and experience papers invited, to furnish a review of evidence of the influence of fish behaviour on:

(a) Liability to capture
(b) Distribution
(c) Reproduction
(d) Growth
(e) Natural mortality

Material in these papers would not only clarify ideas on these questions, but most probably would also provide a basis for establishing some priorities among different lines of research indicated as necessary by discussions.

The implications of the second question were self-evident, but for fisheries biology two special aspects required attention. Firstly, how could there be quantification of observations on fish behaviour with regard to the consequences listed above; secondly, what measurement of environmental factors determining behaviour needed to be made to permit predictions of fish behaviour and hence, more especially, of its consequences to the dynamics of fish populations.

Analysis of Subject Matter

In order to provide a framework for effective discussion of the foregoing aspects, the subject matter was broken down as follows.

1. The elementary actions:
   - Of the whole organism:
     - Movements.
   - Of part of the organism:
     - Movements
     - Noises
     - Colour change
     - Electric discharges and potentials
     - Shedding of sexual products.

2. The basis, control and integration of behaviour:
   - Physiological state and its compulsions
   - Nervous and chemical control
   - Instinctive mechanisms and drives
   - Learning.

3. Kinetic, toxic and reflexive responses to stimuli; being patterns of actions, composed of one or more elementary actions:
   - Responses to mechanical, visual, chemical, electrical and thermal stimuli.

4. The patterns of behaviour:
   - Migration, habitat selecti
   - Aggregation and social rel generally
   - Feeding
   - Reproduction and care of
   - Maintenance activities (tation to the average cond of the habitat and adjustm extremes).

5. Behaviour research:
   - Experimental research; tioned reflex
   - Field observations of beh patterns
   - Analysis of distribution r
   - Presentation of results

Arrangements for the Meeting

It was proposed that the discussion Symposium should be based on two sets of p of which those of the first were to be backg review papers prepared by special consu and those of the second, experience paper tributed by research workers. To clear g for this meeting and also to prevent dupli of material in experience papers, FAO arr for the preparation of background papers following subjects:

(i) Components and determina behaviour dealing with the three divisions of subject mat

(ii) Patterns of behaviour

(iii) Methods of research

(iv) Terminology in behaviour res

It was intended that the Symposium be a "work" meeting which, starting fro analysis of subject matter presented in the ground papers, would consider a numb experience papers, dealing chiefly with re in progress, and would seek to reach conclu carrying conviction, with regard to the n described under the objectives of the symp It was hoped that the Symposium would in practical terms why it was necessary to out behaviour research and help to identi

ts, on the whole frame of reference of this ect, at which research could most profitably irected within the context of fishery pro- s in the Indo-Pacific area.

Consequently the experience papers ed had to be essentially in note form setting he objectives, plan and methods of projects search. Results as such were not wanted, pt perhaps by way of example, because the lusions being sought concerned not the re and causes of behaviour but the influence haviour on fishing (in the broadest sense) the role and nature of research for elucida- of this relation. If the strategy of research l thus be clarified, the available research irces of the region could be more effectively oyed and practical tactics evolved.

cipation and Procedures

The symposium was convened on behalf members of delegations and observers atten- the IPFC Meeting. Following the practice e Council in previous years, the Symposium open to scientists and members of the public e host country, and visitors there, who might to participate.

The Symposium was held during two ings of the Council Session; although it was attended only few of the participants had experience in behaviour research and in equence the discussions related chiefly to ples of the interest of behaviour research ishery studies, and the conclusions drawn ed only to these matters. In the report of ession the Council recorded the Symposium llows:

> "The Council adopted the report on the Eighth Session Symposium "Fish Behaviour with particular reference to Pelagic Shoaling Species" by the Convener, Dr. F.D. Ommanney, noting that the results of studies on fish behaviour were applicable to the industry through the development of fishing equipment and increasing the catch efficiency of existing fishing equipment, through the location of fish concentrations and through the formulation of management programs. Fisheries biologists still lack much of the ordinary fisherman's knowledge of fish behaviour and accurate field observations properly recorded should be made. Care should be taken that conclusions in relation to fish behaviour under natural conditions should not be based solely upon observations made on fish in aquaria."

In addition, the Council resolved that the papers of the Symposium should be forwarded to the present writer for editing and development into an integral volume that might be of value to workers of the Indo-Pacific region as a guide on behaviour research. Although circumstances had prevented us from attracting a set of papers covering this field more or less fully, and, had limited the discussions during the Symposium itself, we had hoped that correspondence and discussions after the Symposium might nevertheless draw some further contributions that would round off this material. Unfortunately we were in this also defeated and in the event I have been obliged to fill certain gaps myself with a theoretical discussion of aspects not treated in the Symposium papers and more especially to write some introductory sections in order to create an integral whole. Obviously this does not make a comprehensive whole and I can only hope that this report may prove to be a useful preliminary review of the field and that it might provide a basis from which a more exhaustive and authoritative study might be developed in the near future.

1. THE NATURE OF BEHAVIOUR

1.0 Introduction

Behaviour is defined in the Shorter Oxford English Dictionary as: "1. Manner of conducting oneself... 2. Conduct: course of action *towards* or to others... 3. Handling: disposition *of* (anything); bearing (of body)... 4. *transf.* of things." Consistently with this definition the term 'behaviour' is applied to living organisms and parts thereof, and to inanimate bodies, and, by still further transfer, to representation of physical entities as in statistics (*e.g.* "the behaviour of a cost-of-living index"). In this broad sense the term signifies change and time; it also implies individuality: for example, the behaviour of a statistical time series is thought to be individual, if not unique to it.

However, it is clear that different kinds of behaviour are intended in each of the above usages, and that the differences are essentially those that distinguish the groups of *things* to which the term has been applied. Thus, whereas the behaviour of a rowing boat in a choppy sea may be fully described, physically, in terms of its movements in response to the waves that buffet it, and the boat itself has no means to react other than in direct response to the waves, the behaviour of an animal refers to conduct of a living being, that has some consequence to the animal itself and in whose control the animal can participate by internal means. Obviously, an analysis and description in only physical terms, of the movements made by an animal does not constitute a complete account of its viour. Behaviour of animals is significant a albeit the significance of some actions m be yet apparent. The study of behavio volves the description of actions, a sear significance and some analysis of consequ

Therefore, whilst we could go som with Baerends who has written (1957) behaviour is built up of movements of musc most objective description of the perform mentioned above [various examples o behaviour] would be one in terms of muscl tractions and relaxations", we might do s as a first step in analysis, recognising tha an account would somewhat resemble proj of a film whose sound track had ceas function. Moreover we must keep in min behavioural actions are not solely mus Acts such as emission of light and of ele discharges, change of colour, and the mak sounds, form part of the patterns of actio constitute behaviour, but properly speaki not movements in the sense that swim leaping, flying and so forth, and the move of fins, jaws, gillcovers and other organ For the purposes of this discussion we regard behaviour as consisting of patte actions of all kinds, and we shall find it first to systematise our terminology of actions, and our views on their nature.

1.1 Elementary Actions

It is obvious that the total of behaviour is made up of a complex series of actions by morphological elements, from molecules up through various morphological levels to the entire organism. It is equally obvious that, insofar as there is a distinction between the things denoted by the terms physiology and behaviour, our part of this series is physiological and the other behavioural. The dividing line between these two is marked by a criterion having regard for the immediate consequences, of the action, external to the operator. Thus, the consequence of contraction of a motor unit is biochemical and located in the *milieu interne* whereas the consequence of fin movement is to some extent in adjacent organs and tissues, and in the *milieu interne*, but also in the external environm the organism. If the action of an organ, o of part of it, can have an external environ influence of subsequent consequence f organism it may be regarded as an elem behaviour if not it is to be regarded as p logical.

Thus we define a behavioural act some change in the position, posture or s properties of an organism that results change in the relations between itself a environment, or enables it to accommo change in the environment, with consequ of some kind that rebound upon the org itself. It is generally presumed that the vioural action of the organism in any part

ıtion is of a kind to produce a change in its ronment from which the consequences will e to preserve the animal and its functions, t is obvious that often an organism's own ons lead it into hostile situations; again some tions lead to completely inappropriate ns (displacement actions); finally the possi- of completely non-significant action cannot cluded. Therefore, whilst we shall include ubsequent consequence to the organism" in the definition of behavioural action we ot assume that the consequence will be rable, nor need we assume in the organism ntention to achieve the consequence.

Considering actions in the series written t the beginning of this section, we shall n with the simplest actions that have obvious parent ecological significance.

We can make a primary distinction, among e actions, between muscular and non- ular acts. In such a system, which would w Baerends somewhat closely, further sub- ion would be made according to sets of les, or particular organs, activitated; within subdivision further classification would be d on description of the type of action, for ple, the speed and rhythm of a fin movement, e intensity and extent of a colour change. Such a classification would be completely free of interpretation of the significance of these actions and most probably would be an extremely useful stepping stone between physiological (and deeper) analysis of the bases to behaviour and the broad, ethological description of these phenomena.

Moving up the series we shall recognise each action as being integral and may classify actions according to their physical effect whilst disregarding both the stimuli in response to which they were initiated, and their "purpose" or ecological consequence. Thus, any of the types of action that result in a change of location (*e.g.* swimming, leaping in air, etc.) may be in pursuit of prey or flight from enemies, or for other purpose. In this system the primary subdivision must be into actions of the entire body and action of part of it. Analysis at this level is considered in the following two subsections.

Beyond this level we must consider both stimulus or motivation, and "purpose" or ecological consequence, and hence we enter the level of recognizable patterns of behaviour discussed in Section 1.2. The relation between these levels of action is indicated in the following table modified from Baerends and Baerends-Van Roon (1950):

t behavioural level	*2nd behavioural level*	*3rd behavioural level*	*4th behavioural level*
	vertical digging	building the nest	
	horizontal digging		
	lateral display	intraterritorial fighting	reproduction
	tail beating		
	frontal display		
	butting		
ovements and	circling		
ges of individual	mouth fighting		
organs	attitude of inferiority		
	biting		
	jerk swimming	boundary fighting	
	frontal display		
	advancing and retreating		
	mouth fighting		

1st behavioural level	*2nd behavioural level*	*3rd behavioural level*	*4th behavioural*
Movements and changes of individual organs *(cont'd)*	symbolical inferiorism	courting	reproduction
	jerking, quivering		
	nipping,		
	formalised digging		
	skimming		
	fertilising, spawning		
	tail fluttering		
	braked exaggerated swimming beats		
	attitude of willingness of the female		
	leading		
	following		
	tail wagging		
	circling		
	jolting		
	digging	caring for offspring	
	aerating		
	nipping		
	leading		
	ingesting swimming food	feeding	nutrition
	browsing on, and ingesting bottom organisms		
	grazing on algae		
	chafing, jumping, tail-wagging	comfort movements	well-being
	flickering the fins		
	mumbling, yawning		
	floating in the water	resting	
	lying on the bottom		

1.11 Motion of the entire body

When we come to consider "what can a fish do?" we find that whereas at first we think of 'swim', there is quite a range of complex movements of the animal as a whole. We find, in fact, that we must recognise that lying passively in water, perhaps sleeping, is part of this range, and our schedule of movements must include 'no-movement'. At least for other animals, and apparently for some fish (and it is not known that it is not for all fish), sleeping behaviour is a part of behaviour pattern, perhaps as much as is waking behaviour. Again there are many s that at times assume passivity, becomin tually motionless, for one or another of a v of reasons: in defence, as a condition pre to attack, or for transport.

It is perhaps as well to dispose at o a difficulty concerning the significance term 'swimming' in this work. It is of true that unless a fish is out of water it is ming. Nevertheless, the other acts that performs whilst swimming may be cons separately; for example, the movement of the stickleback *(Gasterosteus aculeatus)* in d

r through the nest that holds its eggs, is times other than swimming, even if at the time the caudal fin of the stickleback (and mably other organs too) are active in deter- ng how its body lies in the water, and their n is linked with that of the pectoral fins. the other hand, swimming of course is may be the whole, of various behaviour rns, some of which, as for example the ship ceremony of *Lebistes reticulatus*, are complex.

The states we refer to here are those h can be considered as involving the entire of the organism. These are movements to fer the body in space, or to use the weight e body to assist in the accomplishment of act (such as that of a swordfish driving word into some other body and that of builders in tearing vegetation) or to hold a particular place despite forces bearing on ich would move it, or lying passively.

These states may be classified in the fol- ıg way:

Movements resulting in change of location

swimming, walking, creeping, skip- ping, wriggling on dry land, leaping, flying, etc.

Movements involved in the performance of some operation

burrowing, digging; pulling; tearing and moving; balancing; displaying

Lack of movement

lying or holding itself passive; at rest or sleeping, being transported, in camouflage or in place of con- cealment.

The study of these states must consider whole organism even if that study must be n down into an examination of the contri- n made by different parts of the body to aplishment of the action. In all of these ns (or lack of movement) the contractions elaxations of the main sets of muscles of ody must be considered; the patterns of ular action varying from species to species e one kind of action, and from action to ı in the one species. Similarly, the contri- bution of fins and opercular apparatus to the actions varies between types of action and between species.

Study of the states listed above may be made on the one hand with regard to the path traversed by the organism and the speed at which it moves, on the other by an analysis of the means by which the movement is accomplished. In the latter there will be analysis of the move- ments of the trunk of the fish and of those of its fins, the shape of the fish will be considered and such dynamic features as displacement curves, streamlines and entering angles will be examined, methods of steering and stabilising will also be considered; the role of mandibular, gill and opercular apparatus in producing propulsive jet streams will also be analysed. Considerable progress has been made with these studies by the use of various techniques, especially of cinematography. Research making deeper analy- sis examines the physiology of muscular function and neural coordination. Such studies do not consider what stimulated the fish to move, or might cause it to stop the motion, nor what the fish might do in the course or at the end of its travel, but these studies often consider the effect of the consequent internal changes on the capacity of the organism to perform its behavioural actions.

However, whilst these studies provide the analytical description of such actions they also seek to measure the performance the organism can achieve with the action. Thus swimming power (of which cruising speed [Fry and Hart, 1948] is a good measure) can be assessed of itself and afterwards considered in the contexts in which it is displayed.

1.12 Actions of parts of the organism.

Here we are concerned with separate actions by organs or parts of the body which do not constitute part of the entire body actions considered in the previous action, and which produce effects other than those produced by actions in which the whole body is involved. These are chiefly muscular actions, but there are other actions in which the muscular element is small or nil. The following classification is proposed:

Actions of

1) lips, jaws, and accessory apparatus, in feeding, in yawning

2) fins, in fanning

3) gill-covers, as part of the feeding act

4) swimbladder, vertebrae, finspines, etc. in making noises

5) generative organs, in copulati shedding reproductive products

6) glands and spines, in injecting po

7) pigmentation system, in cha coloration

8) electrical organs, in giving elec discharges

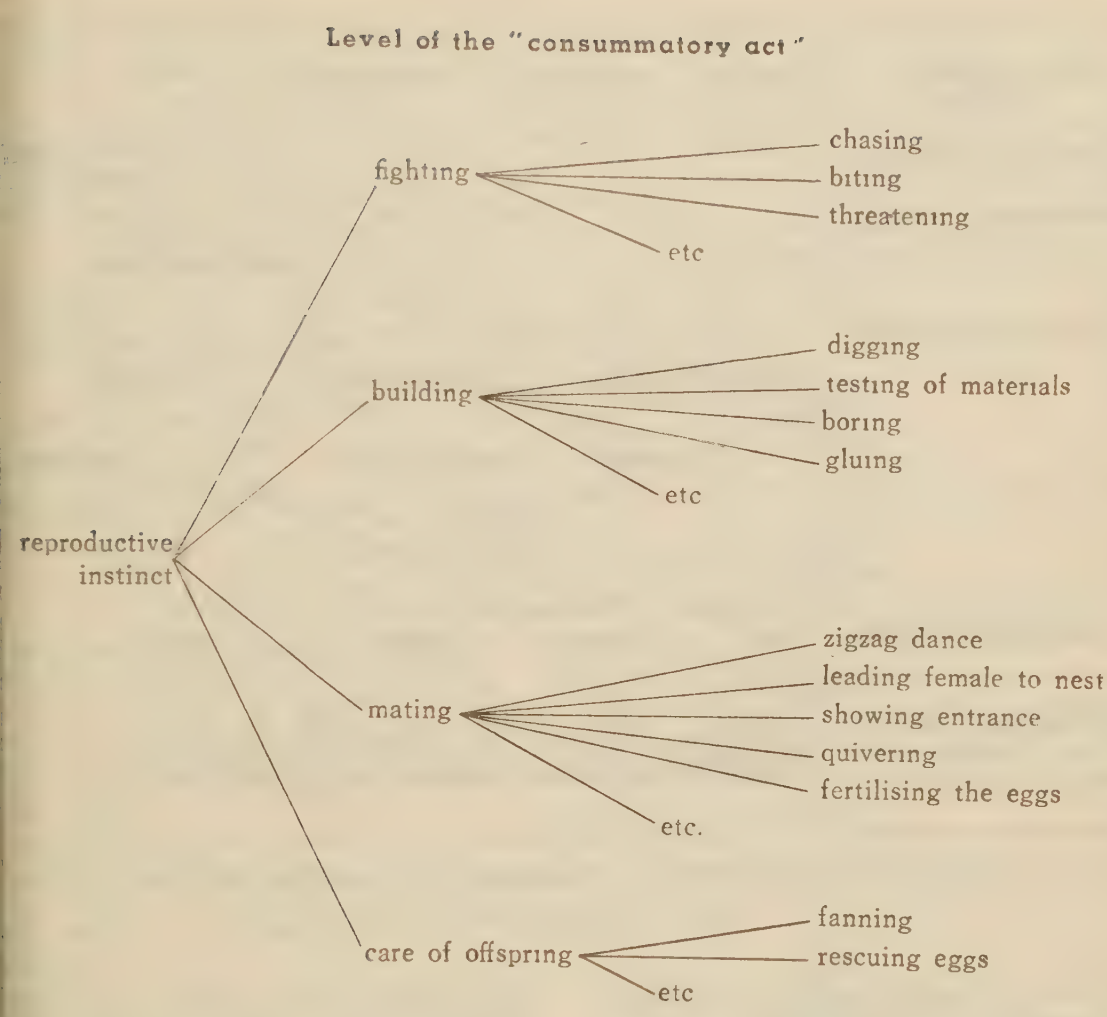
9) luminous or phosphorescent c in emitting light.

1.2 Patterns of behaviour

"By far the greater part of the behaviour of animals falls into the category of instinctive action; only in the higher vertebrates does adaptive or intelligent behaviour play any great role." (Russel, 1938). So far as one of the main purposes of this symposium is concerned, namely the use that the fishery biologist can make (for the ultimate objective of improving fishing or fish-culture) of data on the behaviour of fish in their environment, this statement will be valid. But it will be of less value to him when he turns to the "how?" of behaviour studies, when he must, as times, isolate the reactions of fish to particular external stimuli, making analyses such as those described by Harden-Jones in his paper for this symposium. Tinbergen (1951) reviewing the controversy concerning spontaneous (or instinctive) versus 'reactive' behaviour, wrote "We are at present in a position to say that both opinions contain part of the truth. Behaviour is reaction in so far as it is, to a certain extent, dependent on external stimulation. It is spontaneous in so far as it is also dependent on internal causal factors, or motivational factors, responsible for the activation of an urge or drive." This thus admits to the discussion both the simple reactions, and the complex patterns of broad biological significance. In a physiological approach to behaviour analysis is made in terms of receptors and affectors, stimulus intensity and responses; in the ethological approach analysis is made in terms of internal drive or motivation, releasing mechanisms, sign stimuli, and an hierarchy of behaviour patterns. Clearly both are necessary, but it would seem also to be clear that whilst the physiological approach is indispensable, and has much to contribute, it can provide only a partial account of behaviour. Its role pro is a precursor one, in that it provides an ac of certain of the mechanisms of the basic ponents of behaviour and an analysis c physiological nexus that simultaneously s and determines behaviour. A further r for insisting on maintaining this view c duality of behaviour is that the term 'patte behaviour' can be understood as referri both the patterns of elements of various that compose and contribute to the acts constitute the recogniably purposive acts the patterns of such acts (and pattern of patterns) which constitute the integrated viour of the organism as a whole.

"Patient observation has shown th many movements of a fish can be describe group of fixed behaviour patterns. patterns are innate, stereotyped move performed under certain conditions by all bers of the species in essentially the same Any particular movement occurs in re to a specific internal physiological state requirement, sexual maturity) and in respo definite factors—called releasers—in the nal environment (presence of food, a pot mate). Those patterns of behaviour a characteristic and fixed in form as are the a mical parts of the animal." (Hoar).

One example of behaviour patterns second kind mentioned above, was giv Section 1.1 from the study by Baerends Baerends—Van Roon (1950) of Cichlid f A second example, summarising some o observations of the three—spined stickl *(Gasterosteus aculeatus)*, (from Tinbergen is given below :



It will be recognised that the story esented by this diagram really begins some nce to the right with elementary actions liscussed in Section 1.1), and, as a story of ife of an individual is composed of similar of acts comprising other instincts.

With regard to the right hand side of the am we have first the simple and tentative sis of Section 1.1. Deeper analysis is plified by figure 1, from Weiss (1950), in entre of which are elementary actions of the referred to in Section 1.1. Weiss's system ough not from the paper cited above) similated by Tinbergen (1951) into his rchical organisation in a diagram reproduced gure 2; figure 3 is a detailed representation e of the intermediate levels of figure 2.

With regard to the left hand side of the diagram, and to the sequence of sets of acts, "the task of the neuro-physiologist during the first half of the present century has, of course, largely been to study the mode of integration of numerous simple 'units' of behaviour, such as reflexes (which although simple in their way are, nevertheless, directive), into larger, fewer units which show a more comprehensive directiveness. The stage reached by ethology in this particular task is that at which the behaviour is regarded as composed of about six independent 'instincts'. Nutrition, Fighting, Reproduction, Social Relations, Sleep and Care of the Body Surface are those which at present seem an indispensable minimum in studies on birds and mammals. Each of these instincts is, of course, directive. But is there also any truly purposive element in

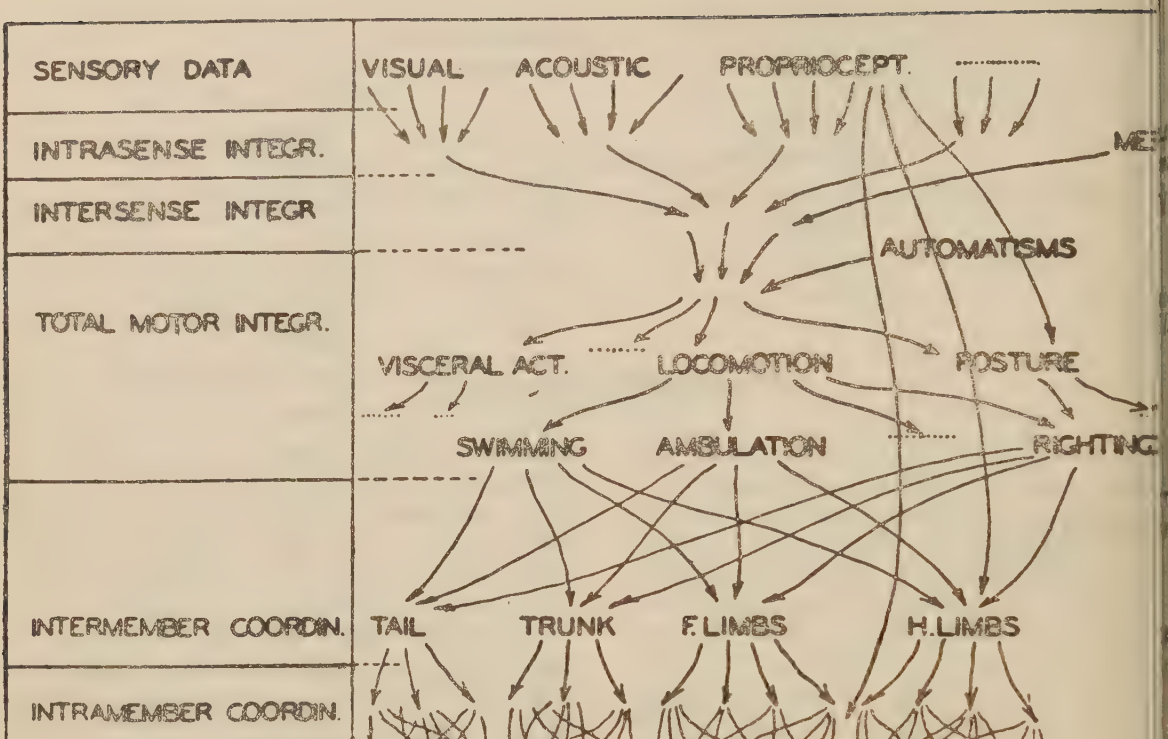
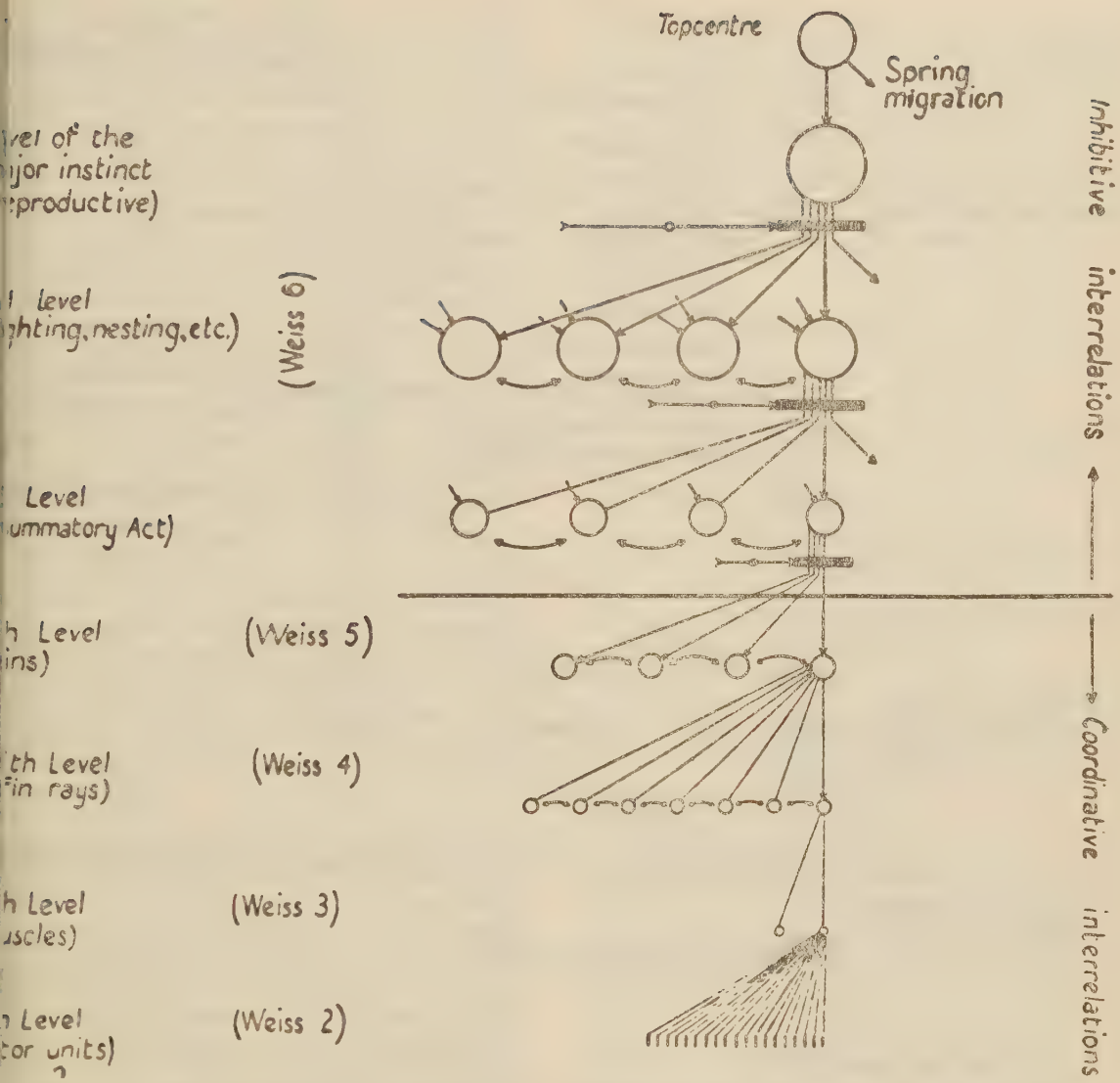


Fig. 1. Diagram of hierarchical organization of central nervous functio
From: Weiss (1950); p. 95.

them or in an over-all centre controlling the whole organism? Is the animal an 'instinct republic' or an 'instinct oligarchy', or is there in any sense a single governing purposive centre of influence? This is the fundamental question." (Thorpe, 1956, p. 8). The first thing to take from this quotation is the simple listing of six independent 'instincts'; this provides a basis to an overall classification of behaviour patterns. But in addition, Thorpe here raises the question of whether this constitutes the totality of behaviour. Later on he says "The view of the instinct—theorist as to the nature of animal behaviour postulates, as in Tinbergen's system, a top centre for each separate instinct; but nothing is said about the relation between the co-ordination of the five or six top centres which are postulated. And so it becomes important to consider how far there is evidence of learning motivated by a general drive quite independent of the motivation of part instincts" (Thorpe, 1956, p. 9), and he dis evidence on the existence of states (such *anxiety*, which he relates to the pain rea which produce general drives other than th the principal instincts. Thorpe's interes in learning, and in the work cited he numerous examples of learning at all lev animal life, including clear cases among He classified learning processes as follow

Habituation
Conditioning
Latent learning and insight learnin
Trial and error learning.

Such processes of course give behaviour patterns features that could arrived at by constructing from reactio through the levels of instinct.



. 2. The hierarchical system of 'centres' underlying a major instinct, iz. the reproductive instinct of the male three-spined stickleback.
From: Tinbergen (1958): p. 125.

Of a different kind is the question that ccur to the fishery biologist who may ask ner the six instincts encompass accurately n features of behaviour with which he is iar, notably the nomadism and migratory e of so many fish. A migration is certainly 'consummatory' act, and yet, is it appeti- ehaviour as that term is defined? Is it ished that a migration that ends in the ductive act began with, as it were, a physiological 'intention' to achieve that act? Or that the salmon returning to sea after spawning does so driven by hunger alone? The table of actions from Baerends and Baerends-Van Roon in Section 1.1, shows 'resting' and 'comfort movements' which presumably lie outside the six 'instincts'. These other movements of course fall within the category of maintenance activities, for which Russel (1938) proposed a scheme as follows:

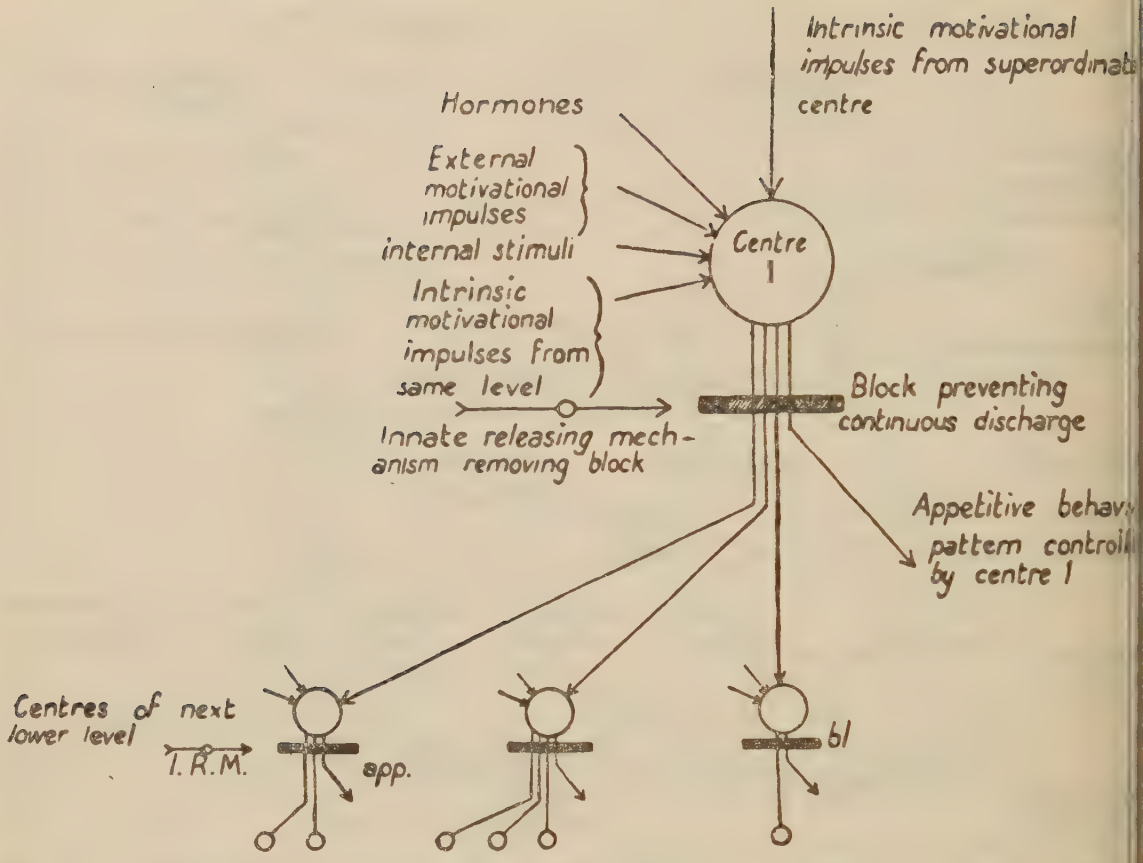


Fig. 3. Tentative representation of an instinctive 'centre' of an intermediate level.

From: Tinbergen (1958): p. 124.

1) Position responses
2) Finding and maintaining the ecological norm
3) Food-finding activities
4) Escape from enemies.

The third of these might be omitted as being of different category and already encompassed under the Nutrition instinct; and it may be that the ethologist would assimilate all four to the six instincts (perhaps by careful definition of the six terms in the quotation from Thorpe), more especially to "Care of the Body Surface".

A further category of behaviour to which reference must be made is that of the displacement and "fall-back" phenomena, conc which Hoar (1958) has written:

"Under ordinary conditions the hie of movements occurs in an orderly and sequence. Under some other conditions, ever, the sequence may be quite inappro and seemingly illogical. One of the mo portant contributions of the ethologist ha the establishment of a general principle respect to these illogical movements a demonstration that they, too, are predi Some of the best examples are to be fou Tinbergen's (1951, 1953) studies of the s back. There is no reason, however, to su that the same principles will not be fou apply to the salmon's behaviour when thi well known as that of the stickleback.

When the male stickleback has prepared t and is ready to spawn, he will lead a female e nest in the so-called zig-zag dance and her the entrance or he will fight another if one intrudes into his territory. If, at ime, a female appears and does not respond m or is removed before he can show her the he will carry out some quite inappropriate ments. Usually he will perform the "fan-" movements normally associated with the pation of the eggs but at this time inappro-e since the eggs have not been laid. Less iently he will glue the nest—a movement h is also quite inappropriate since the nest already been glued when it was built. If ner male stickleback appears and suddenly or is removed the inappropriate responses he same but in this case glueing behaviour ore common.

These inappropriate behaviour patterns been termed "displacement activities". are very similar to the normal appropriate ements although they may be less intense or become ritualised (Baerends, 1957). They r when two incompatible instincts are simul-ously aroused or when the normal releasing tion disappears before the completion of the viour pattern.

Under certain conditions a similar sort of viour may be observed when a fish is strongly rbed. Under these conditions the behaviour been observed to "fall back" to an earlier e of the hierarchical organisation. For ple, if a male stickleback, in more advanced ductive behaviour, is frightened or sub-d to an abnormal lowering of temperature the behaviour falls back to preliminary phases—first to nest building, and, if strongly disturbed, farther back to migration (Baerends, 1957; Van Iersel, 1953). The behaviour, although inappropriate, is predictable and can be analysed."

To summarise, the broad framework on which a classification of behaviour patterns can be constructed may be something like the following:

1. Simple reflexive
2. Instinctive
   a. Nutritional *(includes some migrations)*
   b. Fighting
   c. Reproduction *(includes some migrations)*
   d. Social relations *(includes schooling and parental care)*
   e. Sleep
   f. Care of the body surface
   g. Displacement and "fall back" phenomena
3. Maintenance
   a. Position responses
   b. Finding and maintaining the ecological norm *(includes some migrations)*
   c. Escape from enemies.

2. THE BASIS, CONTROL AND INTEGRATION OF BEHAVIOUR

2.0 Introduction

The basis to behaviour is, of course, anatomical structure and physiological function. The role of anatomical structure would seem too obvious to call for comment, and yet not only must we analyse the elementary actions along some lines such as those described in Section 1.1, but we must recognise that apparently similar actions may differ quite considerably in the muscle contractions by which they are accomplished. Thus, Tinbergen (1951) emphasising this point, compared the muscular contractions of an eel when swimming with these of a fish like *Labrus* or *Sargus*, and with the movements of a male stickleback fanning a nest.

Of the physiological functions Tinbergen *(l.c.)* has observed: "We are realising more and more clearly that the physiological mechanisms underlying instinctive behaviour are much more complicated than we were able to see at the start. Previous attempts at synthesis, such as Pavlov's reflex theory and Loeb's tropism theory now appear to be grotesque simplifications." These functions may be considered from several viewpoints, giving a picture differing perhaps from that intended by Tinbergen's "physiological mechanisms underlying instinctive behaviour" since we are considering also behaviour that lies outside the scheme of instincts.

Firstly we may consider physiological function as the metabolic processes that energise the ostensive acts, or elementary actions. From this viewpoint we recognise that the physiological state of an organism has a simple direct influence on its behaviour; compare for example the swimming power of an exhausted fish with that of one that is not exhausted. There is considerable evidence of the influence of physiological state on the responsiveness of an organism to stimuli: this is an influence on the receptor apparatus, on the integrative apparatus of nerves and glands, and on the effector apparatus. At this level then we are using the term physiological state to refer to metabolic function.

Next we may consider physiological function (chiefly the neural) as the service for intermediating the simple behaviour patterns. Here we refer mainly to the nerve receptors, impulses and signals, but also to the endocrine system.

Next we may consider the physiol
rhythms imposed on the principal developm
cycles of the individual, which are the
bases of 'drives'.

And finally we may consider the 'd
themselves which, although formed and rel
by a complex of forces (most of whic
external to the organism) are esse
physiological in character.

2.01 Physiological States

Analysis of this kind, of a part
species, identifies and describes a seri
physiological states in each of which s
patterns of behaviour are possible, proba
even certain, whilst others are unlikely o
impossible. A classification of such states
certainly be complex since it must accomm
at least three categories of modulations. F
there are those of life-phase, at least of p
productive, reproductive and post-reprod
phases (sapposing the last to exist among
Secondly, there are those that pertain t
existence of a drive and those when no
drive is operative. Thirdly, there are th
particular circumstances, especially situ
which impose a stress on the organism. I
be recognised that this approach is som
more generalised than one based on the c
of 'internal motivation' defined by Thorpe
as "that state of the animal responsible
readiness to perform the behaviour patt
one instinct in preference to all other beh
patterns".

Of overwhelming interest in this ar
are the 'drives', of which Hoar (1958) has w
"a complicated behaviour such as reprod
which occurs seasonally or perhaps only o
the animal's life...is associated with a se
physiological changes (endocrine activit
maturation of gonads) and may require m
of varied activity for consummation. I
case, the many activities are evidently org
as a rigid series of behaviour patterns relea
a predictable sequence. Each behaviour p
may be preceded by a phase of appetitive
iour—lasting many weeks in the case of
tion—before the goal situation is reached.
case the behaviour pattern of the goal sit
has been referred to as the consummatory

The matter is perhaps more easily alised by thinking of three major levels of nization: the drive, the appetitive behaviour the consummatory act. When a salmon hes a particular size or age, internal physio- al changes prepare it for the spawning act. wning may occur several months after initia- of these changes. We believe that the ges are based on endocrine activity and are gered by changing light and temperature. nittedly, there is little detailed information hese physiological changes, but it is abun- ly evident that something is happening in the organism which makes it progressively e likely for the expression of behaviour erns associated with reproduction. This has n rise to the concept of 'drive', broadly ned as 'the complex of internal and external es and stimuli leading to a given behaviour' orpe, 1956; Baerends, 1957). The anatomical hysiological nature of this 'drive' is unknown the fact that something is happening in the which makes a specific behaviour more likely ccur cannot be doubted. Its development ssociated with appetitive behaviour which be prolonged. This culminates in the goal iation and the consummatory act." Two, or aps three, of these drives command a large portion of the adult life of an organism; these the reproductive and nutritional (hunger), which perhaps should be added search for ogical norm.

2 Nervous and Humoral Control

The discussion of the preceding para- hs, and, in fact, of all the papers of this posium, shows the difficulty of dealing rately with any of the 'parts' of either the aviour patterns or the underlying mecha- ns; few of these parts are only and exclusively se or effect, agent or subject: most are effect hange at one level and cause of change at ther. This is particularly true of the elements e internal (nervous and humoral) mechanisms ch subserve, direct and control the acts that e up behaviour; hormone production is in- ed by certain events internal and external he organism and the hormones in the blood rcise an influence over the organism's sub- uent behaviour. The functioning of these hanisms is subject to two principles.

The first concerns the intensity and racter of the stimulus. Responses to stimuli must be considered in two categories; firstly, "the response shown by changes in the locomotory activity characteristic of appetitive behaviour" as discussed in the paper at this Symposium by Harden-Jones; secondly, the 'sign stimuli' that release, or contribute to the release of innate behaviour patterns. With regard to the first, Harden-Jones has discussed the various levels of stimulus and of intensity of response, and the variation of these with physiological state of the organism. With regard to 'sign stimuli', and the *gestalt* significance of these, Tinbergen, Baerends and others have made detailed analyses of some reactions in fish.

The second principle is that of heterogeneous summation. "... releaser information related to some behaviour patterns is sometimes received through more than one sensory channel. For example, the spawning of the pike is triggered by a rising temperature (lateral line receptors) when the fish are in the presence of a particular type of vegetation (visual receptors). What actually happens in such cases depends on the way in which these stimuli are summed in the central nervous system (heterogeneous summation). Under normal conditions a certain amount of information is received through each sensory channel, but a release of the behaviour pattern may also occur when one of the sensory channels receives little or no information provided that the other is strongly stimulated. In other words, the release depends not on which of the pertinent stimuli are received but how many of them. In the case of the pike, spawning may occur if the temperature is high even thoug the vegetation is sparse. A similar releasing mechanism seems to operate in the salmonids where falling temperature and the presence of a certain type of gravel form the releaser for spawning (Fabricius 1953)." (Hoar 1958).

2.03 Instinct and Learning

Tinbergen's synthesis, represented by figures 1.1 and 1.2, shows how the movements (and other actions) of behaviour construct, through the operation of centres at a succession of levels, into a hierarchical organisation, or innate patterns of behaviour which, in the words of Hoar (1958) "are as characteristic and fixed in form as are the anatomical parts of the

animal". This means at the least, that there is a genetic configuration that determines for the species both the nature and the sequence of responses, internally and externally, to features of the situations in which the organism finds itself. Nor is the fixity of these patterns lessened in significance by the displacement and fall-back phenomena referred to in Section 1.2. The value of Tinbergen's synthesis, and of the contributions made in this field by Baerends, Brett, Hoar and others, lies in establishing that behaviour is in general integrated and has an 'anatomy' constructed of fixed elements.

We have finally to consider whether patterns are completely fixed for each spec are subject to modification in ontogene phylogenetic sense, other than, for the onto tic, the circumstantial plasticity already re to in many places in these papers. There fact, considerable evidence of such modifia First, there is the evidence of learning modes of which have been classified an cribed by Thorpe (1956) (see Section 1.2 f main heads of this classification). Next, is evidence on the evolution of behavio discussed by Hoar (1958a).

2.1 Physiological State: Its Stability, Trends and Fluctuations

Physiological state is the functional basis to behaviour in several senses. First, that the capacity of an organism to perform any act derives of course from its metabolism; second, that the endocrino-neural control system intermediates all receptor-effector chains; third, that normal functioning of receptor and effector elements requires a *milieu interne* of some stability, severe departures from stable conditions have significant influence on those elements; fourth, various internal elements, notably the reproductive organs, undergo cyclical changes which, through the endocrinoneural system exercise considerable influence on the basic behaviour scheme. In certain states an organism performs certain actions in patterns that may be followed through to consummation; but when an internal state is changed, the pattern of behaviour almost certainly also changes.

An organism holds, or seeks to hold, itself in equilibnium, or in some special relation, with its environment. There are many different equilibria involving

a) Satisfaction of internal demands with regard to

(i) respiration

(ii) osmo-regulation

(iii) nutrition

(iv) reproduction

b) accommodation to external pre and influences where these

(i) fluctuate within 'normal'

(ii) cease to be in concord wi internal demands;

(iii) change toward lethal limi

Both the internal system and the en ment are under constant change. The de of the internal system vary from hour t within each day, from day to day within season, from season to season within each and from one bio-phase to another. Mo there is interaction between these sets of tion so that the diurnal range of demand season may differ from the range in an The environment of course has similar var

Animal behaviour, in the sense in we are using this term, is essentially the a of organisms, with regard to their enviro to satisfy internal demands in the f environmental changes. These actions v scope from those of states in which in demand is minimal and environmental con optimal, to those of states in which in demand is greatest and most intense and en mental conditions are most unsuitable fo particular demands. Over the vast ran such possibilities we can usefully recognis principal classes of behavioural state:

State	Internal demand	Environmental conditions
Stable	minimal	optimal [with no extreme variations, diurnal fluctuations with which organisms' physiological rhythms are geared and synchronised]
'Drive' [dominatedby internal demand requiring vigorous action to find or make suitable environment]	high [proceeding along a "driven" sequence]	within favourable range [with no extreme variations]
Stress [dominated by external pressure discordant with internal demand]	any level	unfavourable [abrupt hostile change]
Displacement	high [endeavour to comslete a "driven" sequence]	frustrating [unfavourable value of single or few elements]

Whilst those who study animal behaviour te themselves to the identification, descrip- and analysis of these "states", it is obvious full understanding of such states requires ination of internal demands, and recognition e different forms, directions and intensities ese demands at different times in the life of organism, and under different circumstances.

Activities of maintenance effect, such as red to by Russell (1958) in his classifica- (see Section 1.2) fall under the heading of I: Stable; identification of these in iation with their related environmental itions accounts for a large part of the ibutional picture fo any species. In this there are no metabolic or humoral rentials or gradients within the organism, the environment offers no features of value nd optimal.

Three "drives" characterise fish be- our: reproductive, nutritional, and migratory no-regulatory?), in response to which ronments are sought, modified and accom- ted or coped with. In the reproductive a fish seeks suitable spawning sites; it build nests; it may begin certain actions *-vis* individuals of the opposite sex of pecies. In the nutritional drive fishes out feeding grounds. In the migratory drives, as for example in young fish moving from nursery grounds to the grounds inhabited by adults, particular environments are sought. The physiological bases of these "drives", in terms of metabolic deficits, endocrine accumulations etc., are by no means fully understood, and it is probable that neither the drives nor the resultant behaviour patterns will be fully understood until these physiological bases become elucidated.

A fish may be brought into a state of stress from 'stable' or 'drive' state. The organism then falls under the compulsion of some element (s) of the environment, although its response is largely dictated by the internal demand whose satisfaction is denied. If the environmental threat is biotic, the response is primarily of escape, but if the threat is sustained, respiratory and metabolic disturbances will supervene and the effort to deal with them will dominate, more especially if the biotic threat should be removed.

Displacemet state results from the frustration of a drive, more especially of the consummatory act. Resumption of the behaviour pattern, if and when environmental conditions permit, will take place if the physiological basis of the drive has been sustained and provided that the fish has not been incapacitated by exhaustion or other effect.

Obviously the drives do not appear equally throughout the life of each individual since the division of life into pre-reproductive, reproductive and post-reproductive phases (assuming the last to exist in fish) makes an important distinction between age-groups. Thus it will be recognised that behaviour of fish, as of other animals, is to be seen as a complex fabric d first into the three principal life-phases, each of which are various patterns each e sive of the state in which the organism itself in consequence of the interplay physiological rhythms with the fluct elements of its environment.

2.2 Reactions of fish to stimuli

F. R. Harden Jones*

0. INTRODUCTION

0.1 Appetitive behaviour and the consummatory act

Tinbergen (1951, p. 2) defines behaviour as the "total of movements made by the intact animal" and later (p. 104) discusses the distinction between appetitive behaviour and the consummatory act. Whereas the latter is characteristically a relatively simple chain of more or less stereotyped motor responses, appetitive behaviour is more complex and embraces all the "random", "exploratory" and "searching" movements which bring the animal into the environment or situation where the more specific consummatory patterns of behaviour are played out. Thus the increased locomotory activity shown by mature or sexually maturing fish in the laboratory (Woodhead, 1956) would probably, under natural conditions, bring them into an environment where the specific behaviour patterns of reproduction would emerge. The distinction between these two aspects of behaviour, the appetitive behaviour and the consummatory act, is important here. The consummatory act, the final playing out of the behaviour pattern, is normally released and directed by configurational sign stimuli: given the stimulus situation, the pattern appears; this is the lock-and-key analogy. The intensity of the fixed patterns themselves may of course be modified by environmental stimuli and Hoar (1958) has recently made an analysis of the behaviour of young salmon along these lines. In appetitive behaviour the locomotory activity of the fish is induced, altered or orientated in response to the external change; the fish may start to move, swim slower or faster, turn more or less frequently, or swim in a particular tion. It is this aspect of the reactions of stimuli, the response shown as changes locomotory activity characteristic of app behaviour, that is to be considered here.

0.2 The minimum stimulus

The stimuli that are to be dealt wi mechanical, chemical and electrical, therm optical. The first problem concerns the min level of stimulus to which a fish res Here it is important to make the disti between (1) absolute physiological sensi as determined by electrophysiological techn (2) the minimum stimulus to which the fish trained to respond as determined by condi reflex experiments, and (3) the minimum sti to which the fish can be observed to react natural conditions. The physiological thre is often lower than the biological threshol potential is better than the actual perform Furthermore there can be no doubt that the hold for a particular stimulus will vary wi fish, and to say, for example, that the tempe threshold for a particular fish is 0.01°C., in the same way as one would give a ph constant, is very misleading. The respon the fish will also depend on its physiol condition. Studies on sensitivity logically with the limits of intensity and of qu pass on to discrimination, again of intensit of quality and the change of both in time finally to localisation of the source of a stim It is clear that the problem of sensitivity al a difficult one, and such data as are availab fish are very limited, particularly with resp the discrimination of the change of int and quality of a stimulus in time. Bull (

* Fisheries Laboratory, Lowestoft

narised much of our knowledge in this field. damental data of this sort may have important ical applications, as for example when one s to know the likely reaction of a fish ming into a horizontal or vertical tempera- gradient in the sea, or for that matter into a gradient thrown by a searchlight, or a cone und within the frequency range to which ish is sensitive. Under certain conditions arger and probably faster moving fish might more readily than the smaller and slower ng ones.

Kineses and taxes

Fraenkel and Gunn's (1940) scheme of ses, taxes and transverse orientations seems the best framework within which to discuss reactions of fish to stimuli. Fraenkel and n have their critics (for instance, Dainton,), but, if there is only a handful of re- ces to fishes in their book, this is not use of any omission on their part, but rather ts the need for research. More recently ergen (1951. p. 88) has given an account of different types of orientation movements their lines. A point made by Fraenkel and n (1940, p. 270) which may be emphasised is the difference between stimuli which can t a distance, such as light, gravity, water nts, mechanical vibrations, and an electric all of which can have directional properties; hemical stimuli which will vary in intensity ave no directional properties. While it is hysically impossible that heat can be trans- d under water by radiation, it is unlikely to f significance under natural conditions. re the transfer is by conduction through act, as it must nearly always be, the stimulus be a temperature gradient of intensity out direction. However, where convection volved, and the transfer of heat is by the sion or flow of heated molecules with the ate transfer by conduction, the source may cated if the animal can discriminate the tion of flow. It is clear that while fish t be expected to make directed reactions, is, in response to stimuli which have direc- l properties, only undirected reactions, ses, and a klino-taxis would be expected chemical and temperature stimuli, although po-taxis could take place if a gradient was iently steep for two parts of the animal's to be stimulated simultaneously by different sities.

1. MECHANICAL STIMULI

Mechanical stimulation arises from forces which deform an organism or any of its parts. Included here are contact stimuli, steady or varying pressures and all forms of movement which produce constant or varying angular or linear accelerations. The sense organs involved may be contact receptors, proprioceptors or the receptors of the acoustico-lateralis system; of which the labyrinthine organs are specialised for the detection of accelerations. Dijkgraaf (1952) reviews recent ideas on the evolution, structure and functions of the acoustico-lateralis system. The semicircular canals appear to respond to angular accelerations only, while the otolith organs may respond to any movement involving a change of momentum. The response to gravity, or centrifugal force, is of course to a constant, or varying linear acceleration; while sound waves themselves are mechanical vibrations which subject the otolith organs or the unloaded maculae to alternating linear accelerations. Here some of the reactions of fish to mechanical stimuli will be considered under three headings:

1. Reactions to steady or varying pressures
2. Reactions to water currents
3. Reactions to sound

1.1 Reactions to steady or varying pressures

The pressure changes to which a fish may be subjected may be hydrostatic or atmospheric in origin. The former may be due to changes in water level caused by the rise or fall of the tide or the movement of waves, or by vertical movements of the fish itself. Changes in hydrostatic pressure are much greater than those due to atmospheric pressure of which the most rapid changes amount to only 1-10 millibars, (1 millibar = 1 cm water) per hour. Suggestions that certain fish (Philipsen, 1913; Kyle 1926; Wunder, 1936) show sensitivity to atmospheric pressure changes by increased locomotory activity deserve to be followed up in the light of Dijkgraaf's (1942) experiments with the minnow *Phoxinus phoxinus*, which showed this fish to be able to detect changes of hydrostatic pressure as low as 1.5 cm water. In this case the sensory channel involved was the connection between

the swimbladder and ear, the Weberian ossicles. Knight-Jones and Qasim (1955) found that the larvae of *Blennius pholis*, which have swimbladders, respond to pressure changes of 5 cm water.

Changes in hydrostatic pressure appear to be detected through the change in buoyancy following the expansion or the compression of the swimbladder gas. The fish tends to rise or sink a little in the water and this tendency or movement is probably detected by exteroceptors such as the eye, lateral line, or sense organs in the skin (Dijkgraaf, 1942). However Knight-Jones and Qasim (1955) suggest that some other sensory channel at the moment unknown, might be involved.

Apart from adjustment of the volume of the swimbladder, very little is known about the reactions of fish to pressure or pressure changes. Local pressure changes appear to be important in the detection and location of moving objects (Dijkgraaf, 1947). It might be of interest to study the effect of slow changes of hydrostatic pressure, simulating wave action, on locomotory activity, and the results might have some practical value with regard to the effect of weather on the behaviour and distribution of fish.

1.2 Reactions to water currents

Rheotropism is one of most important aspects of the reactions of fish to stimuli, largely because of the widely held, but quite unproven hypothesis that water currents play a considerable part in orientating and directing the course of their migrations. Strictly speaking, the term rheotropism, which is itself something of a misnomer, only covers the reactions to water flow; but here it is proposed to consider all the reactions a fish might make directly or indirectly as a response to a water current, thus including the so-called pseudo-rheotropic responses such as locomotory reactions to visual stimuli arising from the displacement of the background, and responses to angular and linear accelerations produced by movements of the fish in space. Fraenkel and Gunn (1940, p. 249) give a good account of some of the problems of rheotropism. It is well known that many fish lie head upstream and swim against the current so as to maintain their station relative to the ground. This is the typical rheotropic rea and it is of interest to consider the dif conditions under which it might occur.

1.21 *The Stimulus*

1.21.1 *Water flow linear, at constant vel*

If the fish can see the bottom or external reference point, the response m stimulated visually, but blinded fish will upstream if they come into contact wit bottom, when tactile clues are used. Ho in a stream flowing at constant linear velo blind fish, in midwater and clear of the bo does not orientate upstream but is c passively with the flow (Lyon, 1904, Dijkgraaf, 1933). It must be emphasise fish have never been shown to be orie with or against the flow of a body of moving with a constant linear velocity they are close to or are in sight of the bo On the other hand a blind fish, swimmi midwater, will orientate to a jet of Dijkgraaf showed this reaction was abolis the lateral line was cut.

Thresholds for visual and tactile or tion are of considerable interest. Dijk (1933) found that water currents of the or 20 cm/sec. were required to produce orie responses of blind minnows in contact wi bottom. The threshold for visual orientat probably very much lower. Jones (unpubli found that small pike will follow a m striped background making 360° in 40 mi Under the conditions of the experiment a ground displacement of this order wou equivalent to a water flow of about 0.02 cm

1.21.2 *Water flow linear, but with accele*

Theoretically, it would be expected fish out of sight of the bottom and away fr in midwater, would be able to orientate to a flow since the otolith organs are sensit linear accelerations. However, Lowenstein and Gray (1937) failed to find response to accelerations. Jones (1956 b) describe apparent response of blind goldfish to a acceleration with a threshold of the ord 200 cm/sec^2 but while the reaction is enough, the stimulus to which the fis reacting is not altogether certain. In n conditions fish may be subjected to

elerations whenever they move across velocity dients, which may be present in horizontal or ical planes. Whether the gradients and the ed of the fish are ever great enough to produce elerations of the order to which fish appear espond is not certain.

1.3 Water flow curvilinear, at constant velocity

Even in the absence of visual and tactile huli, some fish will orientate to and swim inst the flow if placed in a body of water ated at constant velocity. Dijkgraaf (1933), y (1937) and Jones (1957b) have described response, the sensory basis of which is not understood. The threshold angular velocity ears to be of the order of 3° sec. for goldfish.

1.4 Water flow curvilinear, but with angular accelerations

Fish should be able to detect and orientate ngular accelerations of the order of 0.5° sec^2, gure arrived at from a consideration (for ussion see Jones, 1957b) of the sensitivity of own semicircular canals. There are obvious erimental difficulties in testing the locomotory tions of fish to angular accelerations and no k along these lines has yet been done.

It is clear that there are several possible binations of stimuli to which a fish might t when it responds to a water current, and t great care should be taken in the interpretation of experimental and field observation. hermore there are very few fundamental on the sensory capabilities of fish, let alone r behaviour, to lend support to the theories t stress the importance of water currents as ctional aids on migration. In particular e are very few observations on the behaviour ish in relation to currents out in the open sea ster, 1938; Jones, 1957a; Bolster, 1958).

Something should be said here about turent (eddying) flow as opposed to laminar reamline) flow. Laminar flow is rarely entered in nature. Turbulent flow has been ned as a "state in which random motion of ller or larger *masses* of the fluid is superimed upon some simple pattern of flow" erdrup, Johnson and Fleming, 1946, p. 90). It vident that turbulence would be detected by sh either as a displacement of its own body space, when labyrinth and possibly visual ptors would be involved, or by water movements over the body surface which might be detected by the lateral line or general cutaneous receptors. The former would take place under conditions of macro-turbulence, the latter during micro-turbulence, but clearly the size of the fish is of importance here. Deelder (1958) has shown how elvers will orientate to a source of turbulence and it is possible that turbulent flow might be extremely important to fish. This is a matter which has hitherto received little attention (but see Mackinnon and Hoar, 1953) and might provide a rewarding field for study.

1.22 The Response

1.22.1 Rheo-kinesis

Water currents affect the swimming speeds of fish. Elson (1939) Davidson (1949), Lowe (1952) and Mackinnon and Hoar (1953) have shown this for trout, salmon and eels. Detailed studies to show swimming speeds over a wide range of water currents have not yet been made, but the problem is by no means simple. The response varies with temperature (Keenleyside and Hoar, 1954; Fry, 1958), between species (Hoar, 1951), and is subject to the effects of photoperiodism (Northcoate, 1958).

1.22.2 Rheo-taxis

The normal response is to turn against the current and to head into it. An exception is the hamlet *Epinephelus*, (Jordan 1917a), which turns side or tail on to a jet; there are probably others. A tropo-taxis is possible if the velocity gradient is such that the fish is subjected to different flows over different parts of the body. Under these conditions a fish may be turned about the vertical axis to line up with the stream and this movement might be detected by the labyrinth. Thresholds for the rheo-tactic response are hardly known, and in spite of all that has been written about rheo-taxis, it is clear enough from Fraenkel and Gunn's (1940) account that very little quantitative work has yet been done. This is a pity in view of the fact that use can be made of the rheo-tactic response to guide fish in ponds, and around obstacles. Clausen's (1931) work is often over-looked. He made a survey of the orientation of different freshwater species to moving backgrounds and found that those which found their normal habitat in fast flowing streams reacted better than those which lived in slower streams or on the bottom. Further work on these lines might prove interesting.

1.3 Reactions to sound

Pumphrey (1950, p. 3) defines hearing as follows: "an animal *hears* when it *behaves as if* it has located a moving object (a sound source) not in contact with it. And *sound* can be defined as any mechanical disturbance whatever which is potentially referable to an external and localised source". This is a wide definition, and for fish includes stimuli received through the ear, the lateral line or by cutaneous receptors, and produced by a range of mechanical disturbances such as turbulent water flow, microseisms, and moving objects, as well as sound waves in the every day use of the phrase. But there seems to be no good reason why the definition of hearing should hinge on the word "located", "reacted to" might be preferable. Pumphrey makes a careful distinction between touch and hearing; the primitive function of the former being the location of moving objects in contact with the animal, and that of the latter the location of moving objects not in contact with the animal.

Sound waves may be picked up by pressure or by displacement receivers and Pumphrey (1940) discusses the general properties of the two types. The distinction between them is important: displacement receivers can locate a sound source directly, pressure receivers cannot. The human middle ear and tympanic membrane appears to function as a pressure receiver, and localisation must be carried out with reference to differences of time, intensity and phase: the efficiency of the latter two methods being frequency dependent. The lateral line and cutaneous receptors of fish are probably displacement receivers. In the ears of bony fishes the sensory hair cells of the macula are anchored to the otoliths which have a density of about 2.93 (de Vries 1950). A fish lying in the path of a sound wave will follow the movements of the medium and the otolith provides what is virtually a fixed reference point from which the fish might be able to detect the magnitude and direction of its own displacement and thus that of the medium.

1.31 Thresholds

The literature on the sensitivity of hearing in fishes has been reviewed recently by Kleerekoper and Chagnon (1954) and Lowenstein (1957). While it is therefore unnecessary to go into detail here, it may be noted that the range of frequencies to which a response has been demonstrated is from 16 - 13000 c.p.s., response to frequencies higher than 2000 c.p.s. seems to be restricted to those fish have the swimbladder, or some other gas ch associated with the ear. There is no qu that the upper limit is well below the freque used in echo-sounders and asdics.

It is interesting to note the exte which the cutaneous receptors, lateral lin inner ear, overlap throughout the freq range to which fish are believed to hear. Alt Kleerekoper and Chagnon (1954, p. 139) there is no proof that the lateral line organs play any part in the perception of vibrations (this really comes down to one finition of sound), Dijkgraaf's (1933) experi with minnows clearly show that they do. minnows were trained to follow a vibrating and the reaction was abolished when the l lines were put out of action. From the pub data, and Pumphrey's (1950) analysis, it as if the lateral line, and possibly the cuta receptors, respond to very low frequencies, the ear takes over at about 100 - 200 c.p.s.

1.32 The Response

Here very little is known indeed. already been mentioned that the latera appears to be the sensory channel through fish can locate a source of a mechanical d bance. But attempts that have been ma guide or attract fish with sounds have, s met with little success (Miyake, 1952; B and Moore, 1953; Moore and Newman, 1956) perhaps is not surprising considering tha field and laboratory work (for literatur Kleerekoper and Chagnon, 1954) suggest th localisation of sound sources above 20-50 is effective only at relatively short range 10-20 cm., and that when it does take plac the cutaneous receptors and lateral line are involved. Dijkgraaf's minnow re which were also obtained at very short were with frequencies of this order. The l line organs, acting as displacement rece may well have been detecting changes in pa velocity rather than changes of pressure.

The dimensions of the fish head and rinth are such that it seems unlikely tha would be able to locate, either by differen time, amplitude, or of phase, the source of a tone within the relatively low range of fre cies to which they respond. Localisation be

er with higher frequencies; whales produce, apparently hear, frequencies up in the acycle range (Griffin, 1955). However, even fish's ear appears to be a poor directional Pumphrey's calculations show that there possibilities in the lateral line. Regnart's 7) earlier experimental work goes to con- this. He observed clear orientations of ing to a low frequency sound source, and reaction was less marked after cutting the al line nerves.

The whole problem of the reactions of to sound, both of an increase in activity and a ge in orientation, is raised by Westenberg's 2) account of the acoustical aspects of some nesian fisheries and even more forcibly by enal's (1958) recent re-examination of the e of action of the Vigneron-Dahl modifica- of the otter trawl. Clearly more work is led in this field.

2. TEMPERATURE STIMULI

There are several different aspects of the tions of fish to temperature stimuli which to the complexity of an already difficult lem. Fraenkel and Gunn (1940, p. 189) give ood account of temperature reactions in eral, while Sullivan (1954) deals with various cts of the temperature reception, require- ts and reactions of fish. Fisher (1958) has ten an excellent essay on the physiology of perature adaptation in fishes. Between them e papers cover the literature thoroughly so e is no point in giving more than the essen- here. There are four aspects or approaches ne problem.

(i) First there is the nature of the recep- and the sensitivity of the fish to temperature; uded here is the electrophysiological work Hoagland (1933) and Sand (1938), the litioned reflex experiments carried out by (1936) and Dijkgraaf (1940) and the un- lished experiments on temperature selection r the interference with sense organs described Sullivan (1954).

(ii) Then there are the temperature irements of fish, with the concepts of accli- ion, equilibration, upper and lower lethal ts, selected temperature and the final pre- ndum. An understanding and appreciation ese terms is quite essential to any approach sh and temperature. Here there is the earlier work of Loeb and Wasteneys (1912), Hathaway (1927), and later Brett (1941, 1944, 1946 and 1956), Fry, Brett and Clawson (1942), Fry, Hart and Walker (1946) and Fry (1947). Other references will be found in the main sources given earlier.

(iii) The means by which fish arrive at and remain within their optimum range depends on their locomotory reactions to temperature stimuli. These may be studied in gradients (Shelford and Powers 1915; Doudoroff 1938; Sullivan, 1954), or as an increase in swimming speed under conditions of different but uniform temperature (Fry and Hart 1948). Such studies are clearly related to the temperature requirements. Sullivan's (1954) review is the best account available.

(iv) Finally there are field observations, sometimes under partly controlled conditions (Breder 1951). Sullivan (1954) gives some references, others are given by Fleming and Laevastu (1956). Ferguson's (1958) excellent review brings together field observations and laboratory experiments. The changes in the distribution of fish stocks in relation to climatic changes, particularly temperature, are discussed by Ahalmann *et al* (1948) and Bell and Pruter (1958). The literature for cod has been reviewed by Wise (1958), and Postuma (1957) has discussed the distribution of herring in the sea in relation to vertical temperature gradients.

It is clear enough that the reactions of fish to temperature are quite complicated because of the various aspects of the problem. Furthermore, it must be remembered, as Sullivan (1954) has emphasised, that temperature may act on a fish in two ways. Firstly, through sensory receptors, and thus the central nervous system, and secondly directly through its effect on the metabolism of the animal. A careful distinction must be made between the two, as for instance in the limiting effects of low temperature on the distribution of fish, when the problem is probably one of osmoregulation (Doudoroff, 1945) rather than a reaction to temperature itself.

2.1 The sensory limits

Bull (1956) and Dijkgraaf (1940) have shown that fish can detect temperature changes of the order of 0.01-0.5°c. It is not known over what temperature ranges differences of this order

can be detected. The threshold for the rate of change of temperature which a fish can detect or to which it will react also is unknown. The evidence (reviewed by Sullivan, 1954) goes to show that the temperature receptors are cutaneous. The nature of these receptors is unknown: Whitear (1952) gives an account of the innervation of the skin in teleosts. While it is clear from Sand's (1938) work that the ampullae of Lorenzini in elasmobranchs may function as temperature receptors, opinion is divided as to whether the lateral line has any such function, and Lowenstein (1957) summarises the evidence for both sides.

2.2 The response

Sullivan (1954) discussed the responses of fish to temperature. It is important to make a distinction between the reactions of a swimming fish which is subjected to temperature changes, either as the results of its own movement through a gradient or changes in the water in which it swims, and the reactions of a fish that is resting, and is subjected to a change in the temperature of the surrounding water. It appears that in the latter case movement is only initiated by sudden temperature changes approaching the lethal level, while modifications of the movements of swimming fish are initiated over a wide range of temperature changes. It is these latter movements that are of importance in any study of the mechanism by which fish select and remain within their optimum range.

There is, at the moment, nothing to be gained by dividing the responses into kineses and taxes. Ortho— and klino-kineses, klino— and tropo—, but not telo-taxes, are theoretically possible. Ortho-kinesis seem to be firmly established (Brett, Holland and Alderdice 1958) but at the moment, that is as far as published work goes. Sullivan (1954) refers in her review to a great deal of unpublished work which makes it probable that klino-kineses and some taxes have been observed, but her account is clearly a preliminary one, which is in some places confusing because terms are not properly defined and details are not given. It is to be hoped that the results of her work will soon be generally available in detail so that everyone might benefit from them and our knowledge and understanding of this aspect of fish behaviour be advanced.

3. LIGHT STIMULI

The reactions of fish to light have the centre of considerable attention, and problem is of great practical importance as behaviour affects, in one way or another, efficiency of most types of fishing gear and i basis of several devices for attracting or gui fish into traps and passes. Most fish prob have an optimum light intensity. Their of activity and behaviour may be modifie the twenty-four hour variations in light inten and this is often expressed as a vertical m tion from deep water during the day toward surface at night. This vertical movement al involves pressure changes and sometimes t of temperature, salinity and are often diff to interpret. Anyone who has worked in field of behaviour, or who has come up ag problems of the vertical migration of fi must have been struck by the fact that little experimental work has been done really helps one to understand what is act going on. No one has yet tried to work c mechanism to account for the vertical migra of fish as Cushing (1951) has done for plankt crustacea. And until some such framewor set up, as a working hypothesis, it is difficu see what experiments need to be done, c interpret the numerous observations that now be made so readily with echo-soun techniques.

3.1 The receptors, and their sensitivity

The eye is the principal, but not the o receptor for light. In a number of fish literature see Healey, 1957) the pineal area other parts of the diencephalon are sensitiv light and may prove to be of considerable portance. The cyclostomes *Myxine* and *Lamp* have dermal photo-receptors, which con with the central nervous system by spinal ne in the former, and through the lateral lin the latter. Dermal photo-reception has b shown in some other fishes (e.g. *Epineph* Jordan, 1917b; *Ameiurus*, van Heusen 1917; negative results were obtained in many o species, Parker, 1909).

From the calculations of Clarke (19 and Denton and Warren (1957), it seems light could be detected by a fish at an inten of about 10^{12} down on full daylight (say a

mc), and deep sea fish one log unit lower. threshold for the pineal or dermal receptors nsiderably higher; for the ammocoete the hold of the dermal receptors is of the order 10 mc (Steven, 1950): in the minnow that e pineal complex ranges from 0.01-0.5 mc arrer, 1928). The wavelength to which fish ost sensitive depends in part on the ab- ion curves of the photopigment which in -water fish differs from those in marine fish, in the latter it differs in deepsea fish those of shallower depths. Brett (1957) ws the literature on colour vision, there is oubt that some fish appear to be able to t colour as distinct from brightness. Very appears to be known about the sensitivity sh to rates of change of light intensity. is unfortunate as the problem is most im- nt. A small change in depth, say 20 m. fficient in coastal waters to change the sity by a factor of 10, and at sunrise and t the intensity at one depth may change a redfold in 10-15 minutes.

The response

3.21 *Photo-kinesis*

Ortho-kinesis and klino-kinesis have not been separated in fish. This is no doubt to the practical difficulty in recording their s; photographic recording is obviously ed in use over the range of intensities h are most interesting. A photo-kinesis been demonstrated in one way or another, e goldfish *Carassius auratus* (Shaw, Escobar Baldwin, 1938), blind cave characins (Schla- nd Breder, 1947) *Lampetra* (Jones, 1955) g salmonids (Woodhead, 1957) and larval ng (Woodhead and Woodhead, 1955).

Diurnal changes in locomotory activity lso indicative of photo-kinesis. But care be taken in interpreting the results of experiments, because changes in the experi- al set-up can completely reverse the rhythm es, 1956a).

3.22 *Photo-taxis*

The term photo-taxis is often very loosely and fish are sometimes described as show- positive or negative photo-taxis because collect in the light or dark. The terms photo- ive or photo-negative are the ones to be in this descriptive sense; a taxis, as with a is, is concerned with the means by which the distribution of the animals is attained. The taxes considered here are the three recognised by Fraenkel and Gunn (1940), klino—, tropo— and telo-taxis. In a klino-taxis orientation is achieved by alternating lateral movements so as to obtain a comparison of successive intensities. A klino-taxis can take place with one receptor and in a beam or steep gradient. Tropo—and telo-taxes certainly occur, but the latter requires what is effectively a point source so the conditions under which it would appear in nature are probably few. Very little work has been done in analysing the mechanism of the orientation of fish to light. Work at sea with lamps may give some information as to the reactions of fish to artificial lights and as to what their optima might be (Blaxter and Parrish, 1958, and Zusser, 1953, who gives some references to Russian work). In Japan, Kawamoto has led a long series of studies on the reaction of fishes to light (summarised in Kawamoto, 1957) which valuable as they may be in certain respects, tell us nothing at all about the fundamental reactions and movements underlying observed behaviour. Recently Verheijen (1958) has re-examined the whole problem of attracting animals to light and has put forward a new hypothesis which seems to bring some sense and order into the many conflicting and puzzling observations that have been made in the past. Verheijen maintains that the attracting power of lamps cannot be satisfactorily explained in terms of an "optimum intensity", or "intensity preferendum" hypothesis and suggests that the trapping effect is due to the abnormal angular light distribution around the light source. Verheijen's paper is long; he reviews the literature critically; theoretical and experimental evidence is given in support of his hypothesis, which will, without doubt, stimulate a good deal of discussion and, one hopes, further experimental work.

3.23 *Transverse Orientations*

Here are included light compass reactions and dorsal or ventral light reactions. The former are becoming of considerable interest because of suggestions that fish might make use of the sun, or plane polarised light, as a means of orientation and navigation.

3.23.1 *Orientation to the Sun*

This possibility depends, fundamentally, on the angular distribution of submarine day-

light. Directionality of light is maintained at least down to 400 m. in clear water; vertical light is more intense than horizontal. The direction of maximum light intensity, as measured by its angle of obliquity with the vertical, will however depend in part on the altitude of the sun. Whitney (1941), working mainly in lakes and sheltered coastal waters, found that light intensities measured in the 90° azimuthal plane showed a narrowing pattern with increase in depth and a relative increase in intensity towards the zenith; a symmetrical pattern was approached in deep water. If this is true it looks as if the depth at which a fish could see the sun is strictly limited to very near the surface. On the other hand Atkins and Poole (1957) found in the English Channel that there was no change in the average angle of obliquity down to 70 m., the greatest depths at which their measurements were made. Some form of light compass reaction might therefore be possible towards the direction of maximum light intensity. It is well known that a fish, resting quietly in a tank or light gradient will face towards the direction of maximum intensity. Hasler (1956) has investigated the ability of the minnows *Phoxinus* to learn to orientate by an artificial sun, and has found that the fish can do so; this line of work is clearly worth following up.

3.23.2 *Polarised light*

Light in the sea is plane polarised; one source is from the sky, the other originating in the water itself. (Waterman, 1945, 1955, Waterman and Westell, 1956). As long as vertical illumination exceeds the horizontal, it seems that movements of the sun, or changes in cloud cover, would produce characteristic changes in the patterns of polarisation, that might provide clues for orientation. So far no results on the reactions of fish to polarised light have been published, but observations along the lines of those carried out by Bainbridge and Waterman (1957, 1958) on crustacea would be extremely interesting.

4. REACTIONS TO OLFACTORY, GUSTATORY AND CHEMICAL STIMULI

In vertebrates the receptors for olfactory stimuli are innervated by the olfactory nerve but the gustatory organs, the taste buds, may be innervated by one or more of the dorsal roots of the cranial nerves, the profundus, trige (V), facial (VII), glossopharyngeal (IX), vagus (X). In fishes the nerves princi involved are the facial, glossopharyngeal vagus. The facial innervates the taste bu the mouth, the glossopharyngeal and v those in the gill region. All three may tribute to the innervation of taste buds they are present over the general body su It has been shown that the skin of the c *Ameiurus* is still sensitive when the rel branches of the cranial nerves are cut: the s nerves may therefore be involved in the reac to chemical stimuli as well.

Parker (1922) gives what is probably the most concise and clear account of the tions between olfactory, gustatory and che stimuli in vertebrates, and Hasler (1954, has reviewed the literature and several as of the problem relating to fishes. But th nothing to be gained by going over this gr again here; Hasler's two accounts, which only in their subheadings, cover the liter and the facts as they are known.

There is some interest in conside in general terms, problems relating to directing or orientating effects that olfa gustatory and chemical stimuli might ha fish. In man, according to Parker's (1922, p calculation, smell is, as measured with a s substance, ethyl alcohol, 2.4×10^4 tim sensitive as taste and 6.0×10^4 times as sen as the common chemical sense. Althou similar experiment does not appear to have carried out with fish it looks as if the thre of smell (for phenylethyl alcohol, about 10^- is very much lower than that of taste saccharose, about 10^{-5} M). Here, as in vertebrates, the olfactory organ is probabl best of the chemoreceptors, and as such i one designed as a distance receptor, its re to taste being analogous to that which acoustico-lateralis system bears to touch a the mechano-receptors.

This raises the problem of the use sense of smell in direction finding; and it i of wide interest, bearing as it does on pro such as finding either food, or the home s or spawning ground and other members o species, and having possible applications as in guiding or repelling fish, and attra them into and holding them in specific with bait, or more subtle chemical means.

A chemical stimulus can vary in intensity, unless there is a current of water to deliver will not possess the property of direction. ere is a current, a reaction may be initiated nically and the orientation maintained by t one might call, for the want of a better e, a rheotropic response. The problem of ntation then becomes that of having some rnal reference point, the bottom, or perhaps, sun, to determine the direction of flow, ss the velocity gradients themselves are cient to provide the necessary information.

If there is no water current to help or is impossible to detect it, the source of the nical stimulation can only be reached by the types of kineses, a klino-taxis and, if the ient is steep enough, a tropo-taxis. The t lateral extensions of the head in the mer-head shark, *Cestracion*, might possibly n adaptation towards this end, the distance een the olfactory pits being sufficient to v them to be stimulated simultaneously by rent intensities. Parker (1922, p. 67) found dogfish consistently turn towards the of the open nostril if the other is ged. This observation, together with the that, apart from the lampreys, the nasal ns are paired, suggests that a tropo-taxis be the mechanism for an orientation to nical stimulus in fishes. Tropo-taxis would ainly seem to be more efficient than klino-s, and in the open sea, either type of kinesis ld appear to be rather inefficient.

Chemical stimuli may well be important to plankton feeders, whose prey, in high sum- is rich in oil and might thus be detected at stance. In view of the possible practical ificance of olfaction in fishes, it might be hwhile carrying out some careful observa-s on the movements of blind fish, with ged and unplugged nostrils, in large tanks the long narrow ones used by Shelford and ers, 1915), and in chemical gradients to h the fish have been conditioned to finding food at the centre.

5. REACTIONS TO ELECTRICAL STIMULI

Fraenkel and Gunn (1940, p. 310) con-red it most unlikely that there were specific ptors for electrical stimuli, and held, on the rary, that such reactions as were observed were due to the direct action of electric currents on the nerve trunks or muscles. In consequence the problem of the reaction of fish to electrical stimuli was not considered in their book. There is of course an extensive literature on the applications of electricity to fisheries biology. Applegate and Macy (1954) have produced a selected bibliography; Cattley's (1955) account gives a clear outline of the fundamental problems with regard to electric fishing. But these more practical aspects are not going to be considered here, and the account will be brief and restricted to the nature of the response, the terms used to describe them, and the thresholds and possible receptors for electrical stimuli.

5.1 The nature of the response; definition of terms

When a fish is subjected to a DC or AC current, the response varies according to the intensity of the stimulation. Johnson (1958) recognises five levels of response.

1. First signs of stimulation; tremors of the fins and body musculature, eye movements, facial twitching.

2. Random swimming movements up and down the field.

3. Controlled movements; swimming to the anode in a DC field; coming to rest in a position parallel to the electrodes and at right angles to the direction of current flow in an AC field.

4. Loss of equilibrium.

5. Total paralysis.

The terms used to describe the controlled movements shown by fish in an electric field do not fit in well with the Fraenkel and Gunn scheme, but they are in such common usage (as the term rheotropism) that it would be foolish to attempt to change things. Galvanotropism refers to the orientation shown by fish parallel to the current lines and towards the anode in a DC field. If the current is reversed, the fish may turn around and go to the other electrode; this is galvanotaxis. Oscillotaxis describes the reaction in an AC field when the fish takes up a position at right angles to the direction of current flow. Van Harreveld (1938) gives references to some of the earlier work.

5.2 Thresholds and the Nature of Electrical Receptors

The nature of the receptors for electrical stimuli are not yet known. The typical response appears to be virtually unaffected by sectioning of I, II, VII, VIII, and X cranial nerves, removal of the skin, or sectioning the spinal cord behind the medulla. The fact that destruction of the spinal cord abolishes the response suggests that the electrical stimulus does not act by direct action on the muscles themselves. However, Kuhn, Schulze and Spicker (1955) found that galvanotactic responses were not abolished after curare injections; but Johnson (1958) found that they were. The results of experiments involving de-afferentation operations and the use of curare are of course extremely difficult to carry out and interpret, and at the moment it seems reasonable to suppose that the spinal cord is involved in the response, and that both peripheral and central receptors are involved.

The intensity of the stimulation needed to invoke the different levels of response is interesting. For 18 - 20 cm trout in a pulsed DC field (duty cycle 0.5), Johnson (1958) found that total paralysis was produced by a voltage only 5 times greater than that to which the fish gave first signs of response; the latter threshold was a potential gradient of 0.1 volts/cm. Experiments with AC give similar results, and the threshold is of the same order of magnitude. The point is that the safety margin, between the first signs of response and total paralysis, is very low indeed, and that if electrical stimuli were to be of some possible biological significance the threshold of perception would have to be considerably lower than it appears to be.

The electrical responses that have been mentioned so far almost certainly have no counterpart in nature; they are seen only in the laboratory or, in the field, in response to artificial stimuli. There are probably no specific electrical receptors, as such, involved. The fish responds because the stimulus is sufficient to have an effect on the fundamental mechanism c nervous system. The reactions, at any ra controlled ones, are forced movements; th has no "choice" as to what it does.

But in the electric fishes this is n case; the thresholds are very much Lissmann and Machin (1958) found that a *Gymnarchus* could detect potential gra of about 0.03 μv/cm. Lissmann (1958 discussed the nature of the possible recept such electrical stimuli, with particular refe to modifications of the lateralis system.

It is interesting to note that the sens of *Gymnarchus* appears to be within an or magnitude of electrical stimuli occurri nature. A stream of water moving horizo across the vertical component of the e magnetic field will induce an e.m.f. in the transverse to the direction of flow, as giv the equation

$$E = VZL \times 10^{-8} \text{ volt},$$

where E is the induced e.m.f., V the velo flow in cm/sec., Z the vertical component earth's magnetic field in gauss, and L the of the water filament (Bowden, 1953). flow of 1 knot (50 cm/sec), and $Z = 0.4$ and $L = 1$ cm, the potential gradient is order of 0.01/μv/cm. In the northern ma hemisphere, the electrical current flows right to left when facing downstream, that the direction in which the water is moving. e.m.f. induced by a water current of 1 k below the apparent threshold of 0.03 μv/c *Gymnarchus*. But in the sea, the eff electrical length of a fish is greater th actual length and the potential gradient re to produce a response equivalent to that obs in fresh water is reduced by one tenth (Ca 1955). This would appear to bring the tion of a one knot flow of water withi sensory range of a marine fish if it h electrical sensitivity of the same ord *Gymnarchus*.

3. RESEARCH ON BEHAVIOUR OF FISHES

3.0 Introduction

3.00 Some General Consideration

Research on behaviour of fishes, especially which is undertaken with a view to applica- of its results to fisheries, must comprise of several different kinds between which a ce must be maintained. A first distinction e made between descriptive and correlative rch on the one hand, and analytical and imental research on the other. A second ction may be made between field research he research that is undertaken in labora- s and aquaria. A third distinction may be between qualitative and quantitative kinds search. Obviously there is much overlap een the classes; thus most field research is tative and descriptive. In addition, further visions may be made according to the types potheses that guide the research and to the s of techniques employed. The hypotheses ominated by three principal approaches as l by Hoar (1958), namely psychological, ological and phylogenetic. Hoar describes rst as purely subjective and describing the d as objective he notes that two vigorous ls of research make this approach: the arative Psychologists, and the Comparative logists. Whilst these several kinds of rch offer each worker a diversity of elements hich to construct his program, authors of s in this Symposium have stressed two s. First, that care must be taken to avoid rrors that may follow from assumptions that ts obtained in aquaria and under experi- al conditions have a direct correspondence what takes place in nature. Although this need not be elaborated here, it may be l that anything that elucidates discrepances een laboratory results and field observations itself be a valuable contribution to the rstanding of behaviour. Second, it has been ed out that work in laboratories and aquaria d be guided by indications of significant rs obtained from field observations.

.1 Descriptive and Correlative Behaviour Research

Under this heading we refer to investiga- in which the researcher observes and ds behaviour and selected environmental factors, and in no way influences or controls either the organism (in any respect) or any element of the environment. Work of this kind is basic to and indispensable for all behaviour research for fisheries. It ranges from observations on the end results, or consequences of behaviour, such as distribution patterns and the general features of schooling, through observations on general behaviour in certain broad situations, such as behaviour during spawning migrations, to close observation of elements of behaviour in response to particular stimuli in particular situations, such as particular postures as a part of a counting sequence. Some of such observations can be made on fish in aquaria, but the greater mass of data derives from field observations. This work provides accounts of the major behaviour patterns, such as the spawning migrations of salmons, and complex patterns such as of the stickleback as described by Baerends and Baerends-van Roon (1950). It also, by correlation methods, gives the first indication of the kinds of stimuli, and the levels of intensity of effective stimuli, that serve either to induce simple reactions or to release extensive patterns. Success in such research depends equally on the accuracy of the behaviour and on skill in identiobservation of the relevance of environmental factors. Whilst descriptions can be made of fish engaged in some activity or the another, a broader significance is given to such descriptions if the attendant circumstances are described. Statistical analysis may be used to test the reliability of associations that appear to be demonstrated in such work. On the side of the behaviour elements the data are generally in categorical form that is, recording an action made or not made, and the correlations are those that can be measured by ranking individuals according to degree of possession of attributes. However, observation of certain performances can provide measurement data in which case the correlations may be of more directly quantitative form. Fry, in the first section of chapter 3.11 of this Symposium report, gives an account of some methods of study in this field, although most of the methods described impose some restraint on

the fish and properly speaking do not belong under the present heading.

3.00.2 Analytical and Experimental Behaviour Research

Here we refer to research that seeks to determine, by control of either the organism or parts of its environment, or both, the nature and intensity of the response of the organism to particular stimuli. More broadly the determination is of the modifications of behaviour of a fish in a particular situation that can be induced by modifications of one or more elements of its environment. Ideally the behaviour to be modified should be natural but, as noted by several contributors to this Symposium, the environment of even the best aquaria differs in some degree from the natural environment and consequently the behaviour established even after acclimation may not correspond entirely with natural behaviour. Indeed a distinction must be made tion: estabetween physiological and behavioural acclima-blishment of the former may be tested by criteria refering to metabolism, respiration, osmo regulation and simple performances (posture, swimming, etc.), but criteria for the latter are more difficult to find and to test. Hence there is likly to remain some doubt whether under natural conditions a fish would respond to a particular environmental change as it is observed to do under experimental conditions.

Two principal types of experiment have been used in this work: first, the direct stimulus/response experiment, second, the conditioned reflex experiment.

In the second section of chapter 3.11 of this Symposium report, Fry gives an account of some methods of research of the first type. The following brief account of research on commensalism illustrates the development of method and extension of program applied to a particular section of behaviour.

Analysis of behaviour in commensalism

Professor D. Davenport of University of California, Santa Barbara College, Department of Biological Sciences, Goleta, California, has for some years been engaged on a quantitative investigation of the effects of what might be called "ectohormones" on the behaviour of marine organisms, which live in association with others. This work constitutes, in fact, analysis of "chemical tracking" by marine animals. It has sought to show what certain animals are caused to do by factors of specific action, released by other host organisms with which they live in assoc
The behaviour of free living populations of
polychaete and anthropod species has bee
pared with the behaviour of populations o
mensal species.

Some of Davenport's work in this
described in a series of papers under the g
title "Studies in the Physiology of Commens
listed in the bibliography at the end of this

The work first reported (Davenport
consisted of experiments with *Arctonoë fr*
A. pulchra and *A. vittata* to analyse the re
of these polychaete worms with the echin
molluscan and polychaete hosts with whic
lived commensally.

A simple apparatus was used by whi
worms were submitted to a choice between v
types of water, including water from ac
occupied by the hosts. The experimental
tions and results were such as to permit sta
demonstration that these hosts produced a s
diffusable substance which acted as a po
attractant for their polychaete commensals

This work was continued (Davenpo
Hickock, 1951) and extended to *Halosydna*
setosa, to examine the stability, nature and
of the attractant, and showed that the attra
are relatively unstable and that their effect
easily be negated by any disturbance to the

The methods were then applied (Dave
1953) to the polynoid genera *Acholoë*, *Ga*
and *Lepidasthenia*. Responses were elicit
presenting materials held in the tip of fine-p
forceps. *Acheloë astericola* exhibited a po
positive response on contact with its host,
pecten irregularis, a response which, ho
was only relatively specific, being exhibite
number of starfish that do not serve as h
A. astericola in Plymouth waters. The attr
apparently came from all living host tissu
was released in quantity in the stomach;
was extremely unstable.

Extension of this study (Davenport,
using methods the same as those described
first 1953 paper, were then made to *P*
scolopendrina, *Lepidasthenia argus*, *Her*
spinifera and *H. lunulata* showing response
were either relatively specific, or non-speci

In 1955 Davenport reviewed the subj
symbiosis with special reference to integ
factors.

The first apparatus used in this w
shown in Figure 1 (from Davenport, 1950)
apparatus for more complex experiment,
sequently described (Bartel and Davenport,
is shown in Figure 2 Professor Davenport
that more recently he has developed an appa
whihc makes it possible to *quantify* the resp

dividual commensal animals when they are
the influence of host factor. With this
ratus, adaptable for use in the investigation
e effects of chemical substances on the
viour of any aquatic animal, he has been able
ake quantitative studies of orthokineses,
kineses, and taxes in a number of animal
t.

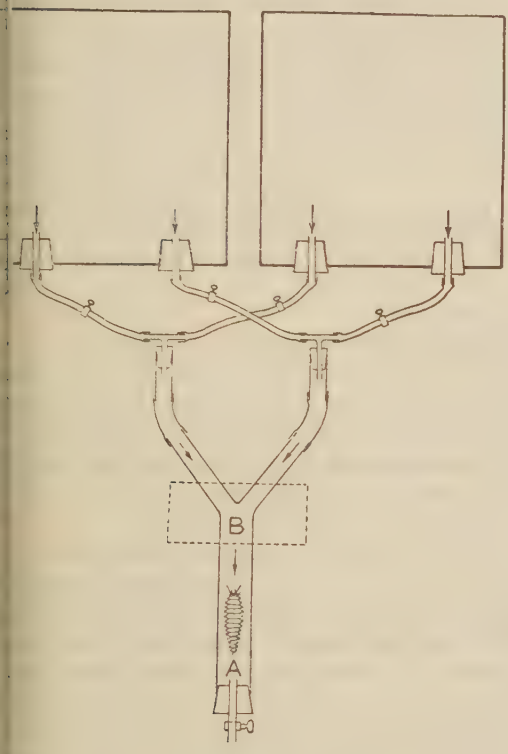


Fig. 1a.
Plan of experimental apparatus.

Fig. 1b.
Enlargement of Figure 1, B.
characteristics as indicated by borax carmine,
ng asymmetrical stimulation of tentacles of
commensal at point-of-choice.

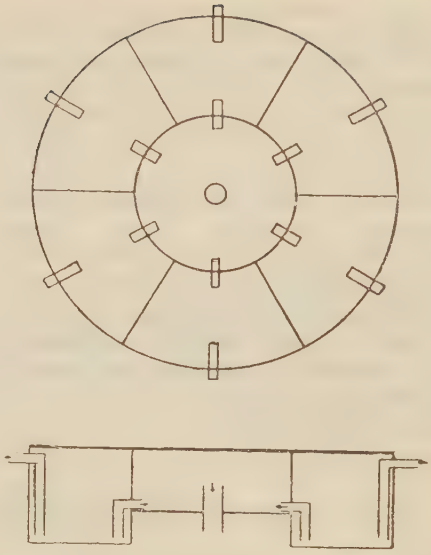


Fig. 2. Test apparatus.
Plan (above) and section (below).

Some of the above investigations have been conducted on the behaviour of fishes but there is no question that the apparatus could be adapted effectively for the investigation of fish behaviour. And in fact the work has been recently extended to one fish species. The results of this work will be published shortly.

In conditioned reflex experiments, certain reflex reactions, such as motor responses involved in food getting, which naturally are induced by particular stimuli, e.g. display of food, may become evocable by other, hitherto neutral or unrelated stimuli. The change, that is, attribution of evocative power to the hitherto neutrel or unrelated stimuli, which is called "conditioning", is effected by repetition "in a constant time and circumstantial relationship" of the original and the new evocative stimuli. In effect, new stimuli are associated with old stimuli and in time become effective substitutes for them. In some cases the subsequent feature of the situation, with which to the organism the stimulus is associated, is rewarding, e.g. food and the reaction is an anticipation of that reward, e.g. in the classical case of the dog, salivation; in other it is a punishment, e.g. a shock and again citing an experiment on dogs, a servere fall in heart beat took place. It will be clear that if a conditioned reflex can be established it can be used as a means of testing the

acuity of the organism's perception of the environmental factor which has been given the new evocative power (the "conditioned stimulus"), because under the experimental conditions the response given by the organism is unequivocal, and directly attributable to the stimulus. Thus, if change of water temperature is made a signal of availability of food so that whenever, under experimental conditions, water temperature changed the fish made appropriate food-getting actions whether food were present or not, then it is possible, as Bull has shown (see Bull, 1958), to determine the temperature differences that fish can perceive by experimental demonstration of the temperature differences to which they will give this response.

3.00.3 Planning Behaviour Research

For the fishery research worker the ning of a program of behaviour researc present many difficulties because of the r newness of this field and because of the tec difficulties of establishing experimental tions of acceptable validity. Observation been made earlier on the balance to be tained between different types of researc especially between field observations and l tory and aquarium experiments. The subsections that follow illustrate approac his problem.

3.01 Research on the Behaviour of Atlantic Salmon at the Biological Station, St. Andrews, N.B.

M. H. A. Keenleyside
Fisheries Research Board of Canada, Biological Station, St. Andrews, N.B.

Several aspects of salmon behaviour are being considered at present. The objectives and methods of attack pertaining to each are listed below. To date most work has been limited to field observations and experiments, but with newly enlarged laboratory space and additional equipment at the Biological Station, laboratory research into salmon behaviour was to begin in 1959. Thus, the following outline is a statement of the research which was planned rather than a report on work which was at that time in progress.

1. DISTRIBUTION

(a) *Objectives*

(i) Determine the approximate limits of distribution of salmon in fresh and salt water along Canada's Atlantic coast.

(ii) Determine the factors governing this distribution.

(b) *Methods*

(i) Compile distribution records for salmon of different ages from published records and by commercial and exploratory fishing. Underwater observations (skin-diving, television, etc.) should be particularly useful in fresh water. Correlate these observations with long-term measurements of such factors as temper solar radiation, salinity, water depth and pH, concentration of oxygen, carbon dioxi other gases, type and concentration of o matter, etc.

(ii) Under controlled laboratory tions determine the "preferred range salmon of different ages for the above char This can be done either in *gradien apparatus*, where the fish spend most ti the preferred section of a tank in whic factor being tested changes quantitively one end to the other, or in *choice-type appa* in which the fish are faced with two or possibilities of which that chosen first is as the preferred.

2. TOLERANCE LIMITS

(a) *Objectives*

(i) Determine the limits of toleran salmon of different ages to temperature, sa oxygen, carbon dioxide and other proper the different types of water in which the during their life cycle.

(ii) Determine the limits of tolera salmon to man-made factors introduced t environment, such as pollutants, sudden pr changes and abrasion at power dams, etc.

(iii) For both (i) and (ii) it is important easure not only those limits within which is maintained but also those within which almon remain active and are able to grow reproduce successfully.

Methods

(i) and (ii) Standard laboratory tests r controlled conditions to measure the upper lower lethal levels for the factors listed.

(iii) Develop a suitable test, such as imum cruising speed, maximum jumping ty, ability to escape predators or speed of th which can be used to determine the s of the various factors tested in (i) and beyond which the fish fail to function nor- y, even though still alive.

MOVEMENTS AND MIGRATIONS

Objectives

(i) Determine the extent and timing of ges in distribution by salmon of different

(ii) Determine the factors responsible nitiating, directing and terminating these ements.

(iii) Determine the relative importance redity and environment in governing the acter of migrations.

(iv) Determine the mechanisms by which on are able to find their way back to "native" ms from the sea.

Methods

(i) Develop suitable tags for salmon of ent ages. Encourage fishermen to report apture of tagged fish. Operate fish traps esh and salt water to record movements of on past specific points.

(ii) Correlate records of captured tagged nd of salmon moving through traps with ographic data. Record age, size and degree xual development of samples of these fish. ne laboratory subject salmon to artifical ges in day-length, temperature, water flow, Using apparatus in which the fish are free vim long distances, determine which envi- ental factors initiate, direct and terminate ations.

(iii) Rear salmon under various con- d conditions, tag and plant them in areas e their survival and times of migration e followed.

(iv) Develop suitable techniques for operating on salmon in the field. Test the effects of severing different sensory nerves on the ability of salmon of known origin to return to their "native" streams.

4. SOCIAL BEHAVIOUR

(a) *Objectives*

(i) Describe the intra- and inter-specific relations (*e.g.* schooling and territoriality) of salmon and other species and determine the mechanisms underlying this behaviour.

(ii) Determine the relation between the social behaviour of young salmon in fresh water and the optimum capacity of freshwater areas to produce salmon.

(b) *Methods*

(i) Describe carefully and analyse, with the aid of films, the reactions between individual salmon and between salmon and other species usually found in the same areas.

(ii) Under controlled laboratory conditions determine the relation between environmental factors and the size of territories, the density and permanence of schooling, etc. This requires a technique for quantitatively measuring the intensity of these social behaviour patterns.

5. FEEDING

(a) *Objectives*

(i) Determine the food preferences of salmon of different ages.

(ii) Describe the methods by which salmon catch their prey, and identify the sense organs involved.

(iii) Determine the factors causing variability in the readiness of adult salmon to take bait in fresh and salt water.

(b) *Methods*

(i) Identify organisms from stomachs of salmon taken in different areas, in fresh and salt water.

(ii) Describe the feeding activities of salmon, both in the laboratory and, by underwater observation techniques, in nature. In the Laboratory use conditioned reflex and other neurophysiological techniques to determine the sense organs used by salmon in feeding.

(iii) By multi-choice tests study the responses of salmon to bait under varying

conditions, both external (colour, shape, size, movement, etc.) and internal (hunger, sexual maturation, etc.).

6. ESCAPE BEHAVIOUR

(a) *Objectives*

(i) Determine the chief natural predators of salmon of all ages.

(ii) Determine the mechanisms by which salmon escape predators, including man.

(b) *Methods*

(i) Review published accounts of causes of natural mortality among salmon. Carry out stomach analyses of potential predators over entire range of salmon distribution.

(ii) Describe and analyse the behaviour patterns used by salmon of all ages to escape predators and fishermen. In the laboratory identify the sense organs used by salmon to escape predators.

7. SPAWNING

(a) *Objectives*

(i) Determine optimum environm conditions for successful spawning.

(ii) Determine optimum sex ratio density of spawners for most efficient spaw

(b) *Methods*

(i) Describe in detail, with the a films, the spawning of salmon. This can be done in large aquaria. Vary external c tions (character of substrate, depth and fl waters temperature, etc.) to determine the of each factor within which optimum spaw success occurs. Develop a test (such a percentage of fertilised eggs which hatch measure spawning success.

(ii) Over a period of years record numbers of adult salmon of each sex ent and the numbers of young salmon leaving a k natural spawning area. By observing sa spawning in the field and in the laboratory c mine the way in which fluctuations in de of spawners affects survival of eggs and yo

3.02 A Contribution to the Study of Fish Behaviour

S. G. Zusser*

Researches upon the behaviour of fishes are increasingly coming into the foreground in our country, because their results are of practical importance for the promotion of fisheries. No effective methods of fish-searching, no improved fishing gear can be developed today, without a knowledge of the behaviour of the fish.

Our report does not pretend to give a comprehensive review of all investigations on fish behaviour, conducted in our country; it merely attempts to throw some light on certain trends of these studies that seem to have a methodological interest.

In the first three decades of our century the investigations on fish behaviour centered mainly on the responses of fish to different stimuli and consisted usually of experiments with one or two species, mostly of freshwater fishes.

A great advance toward a practical a cation of studies on fish behaviour to a fishery problems was achieved in the late th (1937) due to the investigations of Ian Illa vich Messyazev and to his theory of the stru of schools formed by gregarious fishes.

Messyazev has given an exact defin of the two essential conceptions: fish-s and fish-aggregation, which till then were clearly differentiated, every investigator them according to its own notion.

Messyazev defines a fish-school as logical category limited by the species-nu — and length composition of fishes.

An aggregation is a local concentrati several separate schools and is compose fishes of one or more species and of diff sizes. Consequently an aggregation is, gen ly, a temporary formation, heterogeneous

* Moscow, U.S.S.R.

able in regard to its specific — and size — position.

In all water-basins commercial aggrega- of fish depend on certain physical and raphical conditions: such as depth, con- ation of bottom, junction of waters of rent origin and different physical and ical characteristics, areas where currents ot flow in a rectilinear direction but form es, etc.

Messyazev came to the conclusion that ating fishes spend a great amount of energy vercoming the resistance of currents and, all living organisms, need periodic rest.

This suggestion was confirmed by experi- ts (Martinsen, 1937; Aslanova 1952), which ved that fish exposed to a prolonged action rrents seek rest in quiet places formed in one of eddies.

The Canadian physiologist E. Black (1958) s that fish may die from overexertion, their h being caused by the toxic action of lactic (see also Moisseyev, 1957).

The theoretical assumption of I. Messya- hat fish move in isolated schools was corro- ted by many Soviet investigators, who rved fish schools directly from airplanes and els (Golenchenko, 1949; Dmitriev 1939; er, 1949; Krotov, 1938). Subsequent hauls analyses of samples showed that all fish in a ol were of a very similar length. Photographs taken from airplanes both of scools and of egations of anchovies, bonito and herring. mparison of the scheme of currents in the nts and Caspian seas with the distribution h in these basins (1939) proved the correct- of Messyazev's assumption, that commer- aggregations of fish occur in zones of es.

The results of Messyazev's investigations largely contributed to improvement of searching methods and this, in its turn, noted a wide development of new techniques surveying. Observations from airplanes lenchenko, 1949; Krotov, 1938), dirigibles lenchenko and Zusser, 1946) and from erous survey — and research vessels equipped hydro-acoustical instruments, bathystates, lungs and other modern devices, permit the y of the behaviour of fish under natural con- ns.

Messyazev was greatly interested too in experimental work on fish behaviour, namely in studies bearing on the reaction of fishes to external stimuli (temperature, salinity, currents), the role and functions of sense organs in the movement of fish in a current, fatigue and its determination by the accumulation of lactic acid in the blood.

These and other physiological aspects of fish behaviour were studied by J.P. Frolov, one of the nearest pupils of I.P. Pavlov. Frolov, using a method based on the formation of defensive conditioned reflexes found that positive and negative conditioned reflexes to light and sound may be easily established in many species of fishes.

After the publication of Frolov's work many other Soviet investigators became interested in the conditioned reflectory activity in fishes. These investigations are becoming increasingly important as they may help to answer many practical problems of fish management (Voronin, 1957; Prazdnikova, 1952; Malyukina, 1958 and others).

No less important are investigations on adaptive significance of the morphological structure of sense organs and of the central nervous system in different ecological groups of fishes (Baburina, 1955, 1958; Dissler, 1955; Pavolvsky, 1955), as well as on the role played by different receptors in the search for food (Andriyashev, 1941, 1945; Fortunatova, 1949).

An insight into the causes of the formation and disintegration of fish schools and fish aggregations, their structure, stability and distribution, can be gained only by analysing the relation between the organism and its surroundings, by determining the characteristic requirements of a species in regard to environmental factors, its adjustment to variations of these factors, and of the effect of the organism itself on its environment.

It was established by the physiological investigations of Pavlov that animals do not react to all stimuli but only to those which at the given moment act as signals transmitted from the site of stimulation (Pavlov, 1951).

Pavlov's doctrine on conditioned reflexes opened an approach to the knowledge of the relation between the animal and its environment and, hence, to the possibility of controlling the behaviour of different species of animals.

The method of conditioned reflexes permits one to dispense with psychological subjective estimates of animal behaviour and to put the study of the relation between the animal and its surroundings on an objective scientific basis.

Pavlov formulated also the principle of temporary connections in the animal kingdom. During the process of evolution all animals, according to Pavlov, became able to react not only to unconditioned stimuli possessing a definite biological importance, but also to many indifferent stimuli acting synchronously: these indifferent stimuli begin to signal the approach in time of the unconditioned stimuli and thus become themselves conditionally reflectory (Bykov, 1952; Voronin, 1958).

Our biologists consider the behaviour of all animals with a nervous system as reflexes of different degrees of complexity, and ascribe a great importance to individual adaptive phenomena.

Many of our earlier conceptions must be revised in the light of the theory of reflexes.

Thus we are in doubt as to the correctness of applying the principle of tropisms to the study of fish behaviour. Y. Loeb explained the behaviour of animals from the standpoint of animal tropism, by analogy with the tropism of plants. At a later time, he and some other investigators extended this conception not only to infusorians and amoeba but also to such highly organised animals as insects, fishes, birds and even mammals (geotropism of rats). However the conception of taxis does not explain the causality of phenomena in the behaviour of animals with a developed nervous system. On the contrary — in accepting the notion of taxis we merely transfer the phenomenon into the domain of the unknowable for we never could explain what physical and chemical processes determine the formation of instincts in animals.

Let us consider, for instance, the movement of fish toward an underwater electric light, which according to many investigators, is caused by phototaxis, though this does not explain the causes of the phenomenon. If, however, we are approaching the phenomenon from the position of the theory of conditioned reflexes, we may suggest that in the case of plankton-eating fishes, which feed in the daytime, or at dusk, the light of an underwater lamp may act as a signal of feeding, thus causing them to concentrate near the source of light (Zusser, 1952).

Observations both under natural and rimental conditions (Karsinkin, 1951; Soush 1940) proved that fish react to electrical li the same manner as to natural light. A h fish, whose food center is strongly excited swim actively to the source of light, and fe the illuminated zone, whereas replete fish fishes which do not feed at the given tim for instance during the spawning period respond but indifferently to the stimulus of It was observed too, that fishes of dif species and age groups behave different different seasons. All these statements confirmed by direct observations, on fish n underwater source of light (Kashkin, Lovezkaya, 1953; Nikonorov, 1955; Safyanov Demidov, 1955 and other).

T.E. Safyanova and V.F. Demidov that hungry fish swim more eagerly tow light. It was proved by analyses of the sto contents of anchovies attracted by light, they feed within the illuminated zone; 4 the stomachs contained freshly ingested pla organisms. The stability of temporary co tions between light and feeding was conf too by observations under experimental c tions: hungry fishes swam toward a light s more actively than replete ones (Wood 1956; Zusser, 1958).

Thus the complicated phenomenon attraction of fish by underwater light may be understandable when approached from the s point of the principle of conditioned re rather than from that of the taxis-theory analogous conclusion will be reached thorough analysis of any other phenomen fish behaviour, such as, for instance "rheotaxis" or involuntary orientation o in a current. It was demonstrated by obs tions under experimental (Aslanova, 1951 natural conditions (Marti, 1941), that the tion of fishes to currents varies according t stage of development of their gonads. Ther their response to this stimulus will depe which center — the food, or the sex on excited at the given moment.

The hypothesis of the migrating in of fishes (Koslovsky, 1956; Marti, 1954) advanced from the same position of condit reflexes. Instincts are formed by natural s tion, under the influence of external condi and are inherent characteristics of a sp If the conditions of life change, the inst will reorganise too and become more elabo

The modification of acquired instincts is ved by means of conditioned reflexes, which stablished during the life of an individual, laptations to the ever changing conditions e. The paths of migration are fixed during genesis by conditional connections based he finest responses of fishes to changing ical and physical conditions in their natural undings.

The hypotheses stated above have of se to be verified and must be considered as s mere illustrations of our statement that rch work on fish behaviour based on the ciple of conditioned reflexes seems more ising and better orientated than that based e theory of tropism.

Fish behaviour is regarded today as one of the most important problems in the study and the management of our stocks of our commercial fishes.

There are two main lines to be pursued in the study of fish behaviour, namely:

1. The elucidation of biological bases for the development of improved methods of fish-searching in the sea. These investigations include the study of the behaviour of fishes in different stages of development and physical condition, in relation to their natural surroundings, and

2. Observations on fish behaviour in the zone of action of a fishing gear. The results of these observations will aid to develop more selective fishing gear and more effective fishing techniques.

3.1 Laboratory and Aquarium Research

3.11 The Experimental Study of Behaviour in Fish

F. E. J. Fry*

0. INTRODUCTION

As a point of departure we may refer to t's classification of behaviour (1958) outlined Table I. Since the study of behaviour aces everything that an animal does, it will means be covered completely in this rather icted review. This is indeed inevitable in ries work because the various fields have yet received equal attention. Moreover, as ries workers, we are most concerned with omic consequences of fish behaviour rather with fundamental studies from the comparative point of view. Up to the present fisheries workers have been most concerned with ecological and social levels of organisation and of these the ecological level will be emphasised here since the social level has been the subject of a chapter in the recently published "Physiology of Fishes" (Brown, 1957).

TABLE I

ORGANIZATION OF BEHAVIOUR, FROM SCOTT (1958)

f Organization	*Unit*	*Effect on Behaviour*
lical	Population	Localization, territoriality, etc.
	Society	Socialization, dominance, leadership, etc.
smic chological)	Individual	Behavioral adaptation, learning psychological organization, and intelligence.
ological	Organ System	Internal changes, physiological adaptation
	Organ	Sensory and motor capacities
	Cell	Transmission of stimuli; motion
	Gene	Primary stimuli and responses, trait complexes.

Before considering the reaction of the animal to directive factors of its environment on the ecological level, some attention must be paid to the physiological level. That is, the performance of the animal in terms of the acuity of its sense organs and the capacity for performance of the whole animal must be measured and any persistent physiological rhythm that it may possess be made clear. It is most important to know what sensory modalities are operative in each situation (*e.g.* John, 1957) and that fish should not be judged in this respect by human abilities. For example, the recent unequivocal demonstration of the ability of fish to use the sun compass (Hasler *et al.*, 1958, in press) demonstrates the presence of a sense of time in these animals that man certainly does not possess, at least in his present literate state.

epartment of Zoology, University of Toronto.

. *Indo-Pacific Fish. Coun.* (III) :37-42, 1958.

The organismic level dealing as it does with learning in particular, is almost completely disregarded in this review and the genetic level is disregarded except to note that there are specific genetic patterns of behaviour. For example, to cite a personal observation, young pike *(Esox lucius)* when disturbed, such as by capture and transfer from one basin to another, will feign death and hang limply like a dead leaf in the water. Young maskinonge *(Esox masquinongi)* on the other hand do not exhibit this behavioural trait at all. The hybrid between the two species behaves as does the young pike.

1. PHYSIOLOGICAL STUDIES OF BEHAVIOUR

Since Brown (1957) provides an excellent exposition and guide to the literature for most phases of the subject it will not be necessary to make this section extensive. Volume II contains, for example, Bull's (1957) account of the method of measuring sensory acuity by conditioned responses. Two items only will be covered here, methods that have been used for determining diel periodicities and those for measuring capacity for work.

1.1 Diel Rhythms

An example of the influence of normal daily rhythm on the response of fish to a directive factor is given by Kawamoto and Niki (1952). They showed that *Girella punctata* displays an extremely strong light seeking tendency in the day time but not at night (see also Kawamoto and Konishi, 1955). Diel rhythms in fish have been almost exclusively determined by measuring the amount of random movement. Such measurements have been made directly by observation, which would probably be greatly facilitated in the dark by the use of infra-red radiation (Duncan, 1956; Akira *et al* 1953; Woodhead, 1957), by tethering a recording arm to the subject (Spencer, 1939) or by placing a barrier of loose mesh across the centre of an aquarium so that it operated a recorder as the fish disturbed it by swimming through (Wikgren, 1956). Various indirect methods have also been used. Activity cycles have been inferred from changes in oxygen consumption (*e.g.* Clausen, 1936). Pora and Nitu (1952) simply made counts of the opercular movements at intervals. Harder and Hempel (1954) measured activity cycles in flatfish by recording the change in weight whenever they rose from a false bottom suspended from a balance. Reaction movements of a susp aquarium have been registered (Corti and V 1949 a and b). Under favourable circumst such records can be analysed to give the energy output which is transformed int movement of the fish. Finally the water lence set up by the swimming fish has recorded by various mechanical devices (S 1941; Jones, 1955; Fontaine, 1956) or in co temperature chambers by recording the he from a warm bulb (R. R. Langford, pe communication).

Feeding rhythms have been deter by direct observation (Hoar, 1942), and device in which the agitation of a food operated an electric contact. (Kobayashi, and Hirata, 1956).

As will be emphasized again belo not enough to concentrate on the preparat apparatus and on the invention of methods to measure the behaviour under examin Various deficiencies in the conditions othe presented by the apparatus may often infl the response. Thus with regard to m discussed in the present section, Jones (found that minnows provided with shelte exposed to the normal daily changes in displayed a rhythm in activity which wa opposite from that found when they wer prived of cover.

1.2 Capacity for Work

The capacity for work has been u measured by evoking a rheotropic (Lyon, Clausen, 1931) or pseudo-rheotropic (Gray, response to induce the fish to swim in a flu a rotating chamber. An alternative metho used by Oshima (1953) who measured the performed by hooked fish and another by Jo and Fields (1957) who made rough estima recording the struggles of fish taken fro water and laid on a tightly stretched nylo The best quantitative measures that have made in rotating chambers appear to be th Brett, Hollands and Alderdyce (1958) a Paulik, DeLacy and Stacy (1957). These au illustrate their apparatus. Similar methods used by Fry and Hart (1948), Gibson an (1954) and Sörensen (1951). The flume pro has the advantage of providing a better rh tic stimulus since the cues from sight an bulence reinforce each other. In the ro chamber the bottom moves faster than the

at the current-bottom relation has an effect site to that of the visual field whereas in a or pipe the two stimuli reinforce each in the normal way. Katz, Pritchard and en (in press) describe a convenient appa- in which the water circulates in a closed it. The cheapest type of flume is an lar trough such as has been described by chek (1957) and also used by Northcote 3). A large scale recirculating flume has constructed in the behaviour laboratory at University of Washington, College of ries. (Fields *et al* 1954 a and b, 1955 a; s, 1957), and one mounted on a barge and h uses the water in which the barge is d, (Paulik and DeLacy, 1958). Hoar's otactic tubs" (Hoar, 1951; Keenleyside and , 1954) probably represent the extreme in licity for this apparatus.

2. THE STUDY OF BEHAVIOUR AT THE ECOLOGICAL LEVEL

This is fundamentally the study of animal tation. Fraenkel and Gunn (1940) distin- between primary and secondary orientation. ary orientation is the position which an al assumes under normal conditions whether ves or is at rest. This position is with d to certain fixed marks in the environment. ndary orientation is directed movement ted by stimuli from outside which cause the al to shift its position. Both primary and dary orientations may be with respect to inanimate environment or to other orga- s which are within the sensory field of the al concerned.

Fraenkel and Gunn, whose classification is duced in table II, extending and combining deas of earlier workers divide orientation nses into kineses, taxes and transverse tations. Kineses may by considered essen- secondary orientations to gradients in time taxes to gradients in space and will be d together as *Linear Orientations* below, the fundamental method of investigating is to observe the behaviour of an organism appropriate gradient. For an appreciation esent day approach to the study of transverse tations the reader is referred to von Holst) and Hasler and Wisby (1958).

While it is to some extent an academic , it is important for clear thinking to recog- that the circumstances of the environment

TABLE II

SYSTEM OF ORIENTATION REACTIONS OF FRAENKEL & GUNN

KINESES. Undirected reactions. No orientation of axis of body in relation to the stimulus. Locomotion random in direction.

ORTHOKINESIS. — Speed or frequency of locomotion dependent on intensity of stimulation.

KLINOKINESIS. — Frequency or amount of turning per unit time dependent on intensity of stimulation. Adaptation, & C., required for aggregation.

TAXES. Directed reactions. With a single source of stimulation, long axis of body orientated in line with the source and locomotion towards it (positive) or away from it (negative).

KLINOTAXIS. — Attainment of orientation indirect, by interruption of regularly alternating lateral deviations of part or whole of body, by comparison of intensities of stimulation which are successive in time.

TROPOTAXIS. — Attainment of orientation direct, by turning to less or to more stimulated side, by simultaneous comparison of intensities of stimulation on the two sides. No deviations required.

TELOTAXIS. — Attainment of orientation is direct, without deviations. Orientation to a source of stimulus, as if it were a goal. Known only as response to light.

TRANSVERSE ORIENTATIONS. Orientation at a temporarily fixed angle to the directions of the external stimulus or at a fixed angle of 90°. Locomotion need not occur and in any case is seldom directly towards or away from the source of stimulation.

LIGHT COMPASS REACTION. — Locomotion at a temporarily fixed angle to light rays, which usually come from the side.

DORSAL (OR VENTRAL) LIGHT REACTION. — Orientation so that light is kept perpendicular to both long and transverse axes of the body; usually dorsal, but in some animals ventral. Locomotion need not occur.

VENTRAL EARTH (TRANSVERSE GRAVITY) REACTION. — Orientation so the gravitational force acts perpendicularly to long and transverse axes of body. Dorsal surface usually kept uppermost. Locomotion need not occur.

may degrade a taxis into what is a kinesis in the observer's eyes if he is not sufficiently accute in his observation. This was well pointed out by Blum (1934, 1954), who observed that *Harpacticus fulvus* was decidedly negatively phototactic when tested in a cylindrical jar; however when the same animals were put in a shallow dish and exposed to sunlight, the group drifted across the container in the fashion of a kinesis and gethered against the sunny wall of the dish. By Fraenkel's definition they were then positively photokinetic. Blum's explanation was that the paradoxical effect had been brought about by what may be termed a phototactic ratchet. In the shallow basin the larvae had repeatedly retreated to the bottom by swimming away from the light and following the angle of the sun's rays but since they were deflected from the bottom they were finally forced into the brightest region of the container.

Blum's paradox, of course, gives a spurious effect rather than a change in the nature of the reaction but it is easy to devise apparatus that will permit the animal to react wholly by a

kinesis in one situation and in another permit it to react by a taxis, using the same sense organs in both cases. For example the reaction of a terrestrial animal to heat could be tested in two types of apparatus. One type is an open chamber with a radiant source of heat at one end. In this the animal can feel the radiant heat at a distance, since air is a poor absorber of infra-red and can move directly toward or away from the source. If now the animal is placed in a gradient of another type which has baffles to shield the radiant source, it can only react by moving from chamber to chamber sampling the heat in each in turn, a thermokinetic reaction. It can be presumed that in both cases the same thermal sense organs in the skin will be used to mediate the reaction. Matthews (1953) gives an example of a mollusk making such dual reactions in nature. This animal showed a phototaxis when in the sunlight and a photo-kinesis in moving about under the rocks in situations where it was sheltered from the direct light of the sun.

Many circumstances can intervene to influence the reaction of a fish to the situation that an apparatus is intended to present to it. Leaving aside changes which impose substantial physiological stress such as Andrews (1946) reported, the sudden presentation of an organism to an experimental situation may so jar its sensibilities as to render it incapable of displaying the reaction it would make in its normal environment. Sherif (1953) gives an interesting case of such an effect in man. He showed that men presented with a discrimination test suddenly after stumbling and groping in the darkness to reach the place where it was to be given, did much poorer than when given the test under more normal circumstances. A most excellent example for fish, together with an acute analysis was given by Ozaki (1951). He tested the light response of young fish of a species with high tendencies for schooling. He demonstrated that a single individual of this species was incapable of reacting to light of various wave lengths. When paired with another fish of the same species it would react when appropriately oriented to its fellow.

Overfamiliarity with the experimental situation can also disturb the result in terms of reaction to designs of the experimenter. Hasler (1956) found that the irregularities in the metal of a cylindrical tank that were inconspicuous to him were more potent in orienting his fish than was the artificial sun intende the anchor of this universe. Tait (per communication) maintained a group of b trout in a large permanent temperature gra for somewhat over a year, hoping to d seasonal fluctuations in their thermal pref dum. His results appear to indicate tha dominant fish established a territory which held regardless of season, whereas those subordinate and not permitted to establish t selves in the favoured territory displaye expected seasonal change.

2.1 Methods for study of linear orientations

The various types of apparatus for ducing environmental gradients can be class according to the direction of the gradie follows:

Horizontal
  Linear, Annular, Transverse, Ro
  Concentric.
Vertical
  Linear

Each of these types is discussed belo

2.11 Horizontal Linear

This appears to be the first type of a ratus to have been used (Shelford and A 1913) and it has certainly been used for b the greater number of experiments.

The original apparatus of Shelford, simple and typical arrangement. Two suppli water differing in the desired characteristic example temperature, salinity or oxygen con are led to the tank and are introduced at each Both streams flow toward the drain at the c of the chamber. Unless there is a great d gence in the specific gravity of the two stre a satisfactory gradient is obtained with a s boundary at the drain. The Shelford typ gradient tank has been used by Jones, (1947, 1951, 1952), Shelford and Powers (1915) Wells (1914, 1915 a and b).

Linear gradients with a range of temp ture have been described by Doudoroff (1 and Sullivan and Fisher (1953). A light grad of graded intensity has been developed by J (1955) and is figured by Woodhead (1956) similar type was used by Hoar, MacKinnon Redlich (1952). Kawamoto and Nagata (1 arranged their linear light gradient so that it wholly under water.

To avoid the problem of great differences ensity, Baggerman (1957) used water-tight tions which reached from the bottom of tank almost to the surface, as did also ton (1957). In such an apparatus a dark red partition might enchance the transfer of rom compartment to compartment (Hiyama, ko, and Kondo, 1957). In gradients in h the density differences are not so great, as temperature gradients, constrictions at opriate intervals together with vigorous ng in the expanded sections of the tank, satisfactorily maintain the gradient.

2.12 *Horizontal Annular*

The annular gradient is a variant of the r gradient which permits the fish to swim stet inously in the same sense, a circumstance h may often be a great advantage, e.g. Hoar 3). It is essentially two horizontal gradients ed and joined together. The type illustrated ranged for a temperature gradient operated he counter current flow of hot and cold r. Cold water is introduced at one point the overflow is diametrically opposite. The ing water is introduced into a copper tube ered to the bottom of the tank, at the point w the overflow, and leaves below the point e the cold water is introduced into the . The annular gradient used in the author's atory is so valved that the flows of hot and water can be shifted to four appropriate ts 90° apart and the gradient correspondingly ed while the fish are under observation.

Brett (personal communication) produced nnular gradient which was a simple open nel. The advantages of this apparatus its compact size and the ease with which rvations may be recorded by a camera ended above. The temperature gradient obtained by mixing hot and cold water in mpartment below the annulus. The mixed r then flowed up through an outer slot and drained centripetally over the whole extent e inner wall of the annulus. This gradient ates on the same principle as Höglund's 1) fluvarium mentioned below.

The light apparatus of Kawamoto and ayashi (1952) in which a hooded light was nted so that it could travel along a circular may be considered an annular gradient.

2.13 *Horizontal Transverse*

The difference between this type of gradient and the linear gradient is that in its reaction the fish must deviate to one side or other of the path along which it is swimming. The divided trough (*e.g.* MacKinnon and Hoar 1953) is the typical form of the horizontal transverse gradient.

Jones *et al* (1956) placed the drains just behind the drain baffle which is at the end of the channel down which flow the waters with which the fish is to be tested. This arrangement ensures the stability of the gradient in a manner similar to that used by Shelford (1915). Höglund (1951 and figure in Lindahl and Marcstrom, 1958) allows the water to flow entirely across the section of the chamber in which the fish are placed. The extensive work done in the College of Fisheries, University of Washington (*e.g.* Fields, 1957; Fields and Finger, 1954; Finger and Fields, 1957; Johnson *et al*, 1958) was done in divided troughs. Transverse gradients have been the major apparatus used in determining prefence for current strength (*e.g.* Carney and Adkins, 1955).

Collins (1952) used a two choice transverse gradient of temperature and dissolved gases constructed within a stream to test the reactions of a naturally migrating population of anadromous fish.

2.14 *Rosette*

The rosette is a special type of transverse horizontal gradient in which the choice compartments are radially arranged about a central chamber into which they open and in which the fish are placed. Chambers of this type have been used to measure the response to lights of different colours (Kawamoto and Takeda, 1950, 1951; Ozaki, 1951, 1952). Wisby (Univ. of Wisconsin Thesis, 1952) used a four chamber gradient of this type to measure the response of salmon to various odours. This apparatus is illustrated in Hasler and Larsen (1955).

A model for temperature selection is used in the Ontario Fisheries Research Laboratory. There is an odd number of chambers surrounding the central basin. In operation the various

chambers are supplied in random order with water adjusted to temperatures covering the range over which it is desired to test the fish. A screen funnel within the entrance of each chamber allows the fish to enter and sample the water there but still to return to the central section. However, once the fish fully enters the chamber it is trapped. Selection can be measured finally by the numbers trapped in each compartment.

2.15 Concentric

As the name implies, in this gradient isopleths are concentric about a central point. The experiments of Blaxter and Parrish (1958) in which a light was lowered in the ocean at night made use of this principle. A concentric gradient of current exists in a circular pond which is fed at the periphery and drained at the centre; a circumstance that was turned to advantage by Davidson (1949).

2.16 Vertical Linear

The only type of vertical gradient that appears to have been used is the linear, which has been used in experiments on temperature selection (Brett 1952; Ferguson, 1958). The vertical gradient is a convenient method of measuring temperature selection and is the simplest apparatus for this purpose. The gradient can be most easily established by a double heat exchanger (Kendeigh, personal communication) consisting of two parallel coils of pipe. Hot water flows through one of these entering at the top, while cold water is passed through the other, entering at the bottom. Otherwise the gradient can be maintained by circulating only the heating water in the coil and by introducing cold water at the bottom of the tank itself. This latter method is essential in long term experiments where the fish consume a significant quantity of the dissolved oxygen. It is impossible to establish a complete vertical temperature gradient from 0° C in fresh water because of the anomalous expansion of water below 4° C.

Vertical gradients can be establish dissolved substances and a high stability imparted to such gradients by combining with a slight vertical temperature gra Hoar (1954) used a gradient in depth obviously had to be a vertical one.

2.17 Expression of Measurement

The observation ordinarily made experiment on orientation is the numb individuals present in a given segment gradient, e.g. the "gathering rate" of Kaw and his colleagues. These numbers can t compared with the numbers expected to by chance by means of the x^2 test. magnitude of x^2 expresses the intensi the reaction. For examples of this proc see Hoar (1951a) and Fields and H (1954). In gradients where there is a g series of choices such as is ordinarily found in a temperature gradient, and whe distribution of selections is expected to a ximate the normal curve, distributions m expressed in the ordinary terms of mea modes and the usual expression of devi However, this can be done only if the gra has been so extensive that the distributio be completely expressed. Otherwise the persion observed will not be sufficiently gr the distribution symmetrical. Fortunately perature selection is relatively sharp (*e.g.* Garside and Hepburn 1956; Garside and 1958) so that a gradient of some ten centi degrees in the appropriate region is ordi adequate.

Some authors have used the tim vacate or occupy a critical zone as their i Jones, (1947, 1948) used a method based o of Shelford. Ozaki (1952) in his experi with light derived three basic indices fro observations. These were: (1) visits to a chamber multiplied by the duration of the (2) the simple number of visits and (3 number of colours visited. He inferred the of excitement or confusion of his subjects the relative size of these indices.

3.12 Some Notes on Establishment and Maintenance of Atlantic Herring *(Clupea harengus L.)* in Aquaria **

B. B. Parrish, B. Sc.: J. H. S. Blaxter, M. A. and F. G. T. Holliday, B. Sc. *

0. INTRODUCTION

Apart from investigations concerned di- y with fish culture the part played hitherto quarium studies in marine fishery research been a relatively minor one. This is attribut- principally to the fact that in the past marine ry investigations have been concerned arily with field surveys of the biological and ogical properties of exploited fish stocks in static and dynamic aspects. However, as vledge of such properties has accumulated, demand has grown for more precise assess- ts of the factors governing them, and for ter accuracy in measuring them and under- ding their basic mechanisms. There has arisen a need for experimental and observa- al data, many of which cannot be obtained y, or without high coast at sea. Aquarium ies provide a satisfactory means for supply- many of these data and for providing minary guides to the course along which equent field investigations should be ted.

The main types of subject which can be ied in aquaria, either completely or in part, be divided for convenience into four major gories:

(1) Basic physiology: e.g. studies of endocrine systems; food-growth relation; osmotic relations.

(2) General behaviour patterns and responses to environmental stimuli: e.g. response to temperature, light and salinity gradients; shoaling, spawning and feeding habits.

(3) Behaviour responses to artificial physical stimuli: e.g. behaviour to fishing gear components and model gears.

(4) Dynamic properties of populations: e.g. predator-prey relations; density dependent growth and mortality studies.

Each of these categories presents special problems of technique and makes special demands on the aquarium facilities. The most stringent demands are made perhaps by the last category for which aquaria containing large numbers of fish are desired. For this reason, such projects are being tackled with populations of smaller species of fish often kept by aquarists, rather than with species subject to commercial exploitation, for which the demands on space, etc. are too great for representative population characteristics to be reproduced in aquaria. While it may continue impracticable to investigate mechanisms of population dynamics in these species, the difficulties are not so great for many ot the projects in the first three categories. Worthwhile results and suggestions for future programmes of field observations can often be obtained with the species under investigation, using small numbers of fish in easily managed aquaria. It is those types of projects therefore which can be tackled most readily at fisheries laboratories. The programme of aquarium studies at the Marine Laboratory, Aberdeen, has been drawn up primarily to investigate projects in those categories, the principal species of fish at present under investigation being the herring *(Clupea harengus L.)*.

arine Laboratory, Aberdeen.

his work and a further detailed study of the factors affecting feeding in herring are described in he following papers:

Parrish, B.B., Blaxter, J.H.S., and Holliday, F.G.T. 1958. "Herring (*Clupea harengus L.*) in Aquaria. . Establishment". Mar. Res. Scot. No. 5.

Blaxter, J.H.S. and Holliday, F.G.T. 1958. "Herring (*Clupea harengus L.*) in Aquaria. II. Feeding". lar. Res. Scot. No. 6.

The first requirement in a programme of aquarium work is success in establishing the chosen species in the aquarium tanks. For some projects this may involve only keeping the fish alive for a few days, which may present no major difficulties, but for many others it involves establishing and maintaining them as feeding communities for long periods. It is this latter requirement which presents the greatest difficulty with many of the exploited species and which makes the most stringent demands on the general aquarium facilities.

Whether certain techniques are adequate or not for establishing fish will depend to a large extent on the species concerned. Thus the herring is a particularly delicate fish and the techniques used in establishing it in aquaria must take this into account. It is by no means clear why one species should be more delicate than another. In the herring the scales are easily displaced and the integument is thin and fragile. While this may be the prime reason, there may be some nervous factor operating which contributes to the general susceptibility of the fish. For instance, the herring is preyed on by many other animals and thus its well developed behaviour in regard to escape from predators may make it particularly susceptible to shock during capture and handling. In this way it will become more agitated than many other species and may cause itself harm in trying to escape.

The problems in establishing a herring community may be considered with regard to the main stages, as follows :-

1. Capture,
2. Transport to the aquarium,
3. Initial establishment,
4. Maintenance

1. CAPTURE

This is the stage during which most damage occurs, consisting principally of loss of scales, epidermal abrasions and a possible shock effect.

Physical damage can be minimised by using an encircling net, such as a purse seine, ring net or beach seine, for these do not gill the fish and hence do not cause heavy loss of scales. The net should be shot quickly and if pos the fish removed while the net is still in water.

In our experiments, while herring been frequently established after captur beach seine, we have never succeeded with caught by trawl or drift net.

2. TRANSPORT

The fish should be transported from site of capture to the aquarium in glass car or galvanised bins. The distance to t should be as short as possible. Conta should be cylindrical, filled with water and with a lid to prevent splashing, and should smooth walls. In our experiments, herrin cm. long had 7-8 l of water per fish, herrin cm. long 2-3 l per fish. On this basis a sp oxygen supply is necessary only on journeys.

3. INITIAL ESTABLISHMENT

3.1 Aquarium Facilities

Where possible the seawater in which fish are kept should be constantly replaced the sea, to prevent the accumulation of e tory products. Where the water canno replaced a local circulation continually pas the contents of the tank through a sand should be used; this moreover helps to pre blooms of phytoplankton or bacteria. Tra mussels *(Mytilus edulis)* also help to keep water clean.

The minimum sizes of tanks for t purposes seem to be as follows: herring 2 long 3000 - 7500 l, herring 10 cm long 450 - 7 the ideal depth being about 1 m. Althoug use rectangular tanks, cylindrical or ann tanks might be preferable.

The walls of the tank, if concrete, be painted with bitumen-based emulsion pai reduce abrasion, to seal the surface an prevent corrosion of the reinforcing materia is an advantage to have baffles, painted w in each corner of the tank. This appear delimit the extent of the tank and prevent herring swimming into the walls.

It is desirable to control the temperature ie water through a hot wire vacuum switch. used a thermostat controlling a 2 kW tric heating element in a silica glass tube. eater of this power will maintain the tem- ture at about 10° C in a tank holding 1 when the external temperature is below .

Initial Mortality

This may be reduced firstly by careful lling before putting the fish in the tanks. an advantage to establish the fish in sea r of reduced salinity (about 17%°) which is nic with the blood of herring. This reduces risk of mortality caused by osmotic dehydra- through a damaged epidermis A low age bulb may be left switched on at night the tank for the first few days after the fish been captured. This, with the baffles, les the fish to orientate themselves at t.

Initiation of Feeding

Feeding is the main criterion of whether ing have become established or not. We found that providing the tank is of adequate the fish will start to feed under suitable litions after 1-14 days. The best food is ably finely chopped squid *(Loligo)* which is table and easily seen in the water. (Herring ot take food lying on the bottom of the tank). temperature should be about 10° C or more eeding to start. It is a great advantage to herring in the tank that have already n to feed, for their behaviour initiates feed- by newly introduced fish.

4. MAINTENANCE

Feeding

Once feeding has begun, herring must be frequently if growth is to continue. (The tenance diet appears to be about 200 mg/g of fish/week for 20 cm herring and about 300 mg/g of fish/week for 10 cm herring).

The texture and taste (both factors are involved in the selection of food by herring), of chopped squid *(Loligo)* mussel *(Mytilus)* and limpet *(Patella)* appear to be suitable for herring. Supplements to the diet (vitamins, yeast, antibiotics, etc.), which fish will not take alone, may be given by adding them to 15% gelatin made up with a concentrated squid extract.

The food should be given three or four times a day, to allow maximum ingestion, at a rate to obtain the desired growth rate. (3 g/fish/day for 20 cm herring produced reasonable growth and maturation of the gonads, though in our experience the fish did not spawn. Excess food should be siphoned off.

The optimum light intensity for feeding seems to be between 100 and 1000 metre candles. No feeding takes place below 0.25 m.c. and it is reduced outside the optimum limits. There seems to be a diurnal rhythm with feeding intensity being greatest in the afternoon and evening.

The herring appear not to feed below 4° C.

4.2 Disease

The main disease encountered has been fin rot. This may be checked by feeding with terramycin, firstly at a rate or 0.5 mg/g of fish/day and later, as a prophylactic, at a level of 0.1 mg/g of fish/day. The affected parts may be painted with phenoxethol.

4.3 Handling Fish

When the fish are to be moved they should be confined to one end then removed by a hand-net made of plankton netting. The fish may be anaesthetised (before weighing, tagging or using surgical techniques) with tricaine methane sulphonate at a concentration of about 100 p.p.m. for 10 cm. herring and 50 p.p.m. for 20 cm. herring.

3.13 Some Preliminary Observations on the Avoidance of Obstacles by Herring *(Clupea harengus L.)*

J.H.S. Blaxter, M.A.; F.G.T. Holliday, B.Sc. and B.B. Parrish, B.Sc.*

0. INTRODUCTION

Amongst the many factors governing the efficiency of a fishing gear in capturing a particular species of fish, the behaviour of the fish in the vicinity of the gear is the most important. Knowledge of this behaviour is of importance to the gear technologist as a guide in his endeavours to improve gear design and operation, to the fisherman in his attempts to make the best use of the gear available, and to the biologist studying gear selection, fishing mortality and fishing power.

Only recently have serious attempts been made to study such behaviour directly. This has been made possible by the development of underwater observation techniques such as the echosounder, the under-water camera, television and diving with aqualung. These techniques have been applied principally to the study of fish in the vicinity of towed gears, such as trawls and seines, and have provided valuable information on flight responses and escape mechanisms. However, there are some gears for which these methods of investigation are not so suitable; among these are gill-nets, usually fished in darkness to catch pelagic species such as herring.

Little is known of the mechanism of capture of gill-nets and the factors governing it, so that much of the technological development work now in progress with this gear is being undertaken, for the most part, by rather costly and time-consuming "trial and error" methods using, chiefly, comparative fishing experiments.

In the investigation of this problem a method of approach which has received little attention hitherto is to study the behaviour responses of fish to gill-netting in the aquarium. A similar approach was made by Kasaka (1957), and also by Radakov and Nikolaev (1957) studying the responses of coalfish *(Gadus virens L.)* to moving traps. In the aquarium, observations can be made of fishes' respons "obstacles" over a wide range of light int ties, mesh sizes, twine sizes and colours, an importance of sight in the "avoidance" of "obstacles" can be gauged.

Experiments of this kind were, u herring *(Clupea harengus L.)* recently start the Marine Labaratory, Aberdeen; this re deals with preliminary results obtained in

1. METHODS

The experiments were conducted concrete sea-water aquarium tank measu 3.7 m × 1.8 m × 1.1 m. The tank was fitted removable wooden covers and tungsten fila lamps, so that the light intensity could be va between complete darkness and normal inci daylight.

Most of the work was carried out o herrings about 25 cm long, which had live the tank for 18 months and were fully esta hed. Some experiments were also carried ou 18 herrings about 12 cm long.

The barrier or obstacle in each experi consisted of a pattern of horizontal an vertical strands of twine or other material, to a movable wooden frame having the sectional dimensions of the tank.

The fish were usually confined on side of the barrier at the beginning o experiment. In daylight their reactions t barrier were studied in two different ways:

1. by counting the number of fish pas through the barrier during perio 30 minutes without any ext disturbance.
2. by measuring the time taken to all the fish through the barrier a end of the 30 minutes observa period.

* Marine Laboratory, Aberdeen

On sunny days care had to be taken to ɔmise the effect of uneven illumination due adow in the tank. Most of the experiments carried out in daylight but in the later ɛs low light intensities or darkness were . Under these conditions two means were to observe the fish:

1. by taking photographs of the tank every 60 seconds with an underwater camera fitted with electronic flash,

2. by turning on a bright light for five seconds every 60 seconds, the position of the fish being noted by a dark-adapted observer under the wooden covers.

The following aspects of barriers were ed:

1. Type, colour and thickness of material used:—

   (a) Manilla trawl twine-white (0.3 cm diameter)

   (b) Cotton drift net twine-white, green and black (0.05 cm diameter)

   (c) Polyfilament nylon drift net twine-white (0.05 cm diameter)

   (d) Monofilament nylon-almost transparent (0.02 cm diameter)

   (e) Household cotton-white (0.02 cm diameter).

2. Mesh size or the distance between adjacent horizontal or vertical strands. Distances from 30 cm to 2.5 cm were used. Where a mesh was used, it was not knotted. This prevented fish that passed through the small meshes from becoming gilled.

3. The importance of a mesh as compared with its horizontal or vertical components alone. This was studied by taking a particular material and comparing the reaction of the fish:—

   (a) to the material made up as a mesh,

   (b) to the horizontal strands only } the distance between adjacent strands being the same as the mesh size.

   (c) to the vertical strands only }

2. RESULTS

2.1 Experiments in Daylight

Most of the results were obtained in full daylight at light intensities from 10^4 to 10^5 lux.

The behaviour of the herring under "normal" conditions without the barrier was noted at the beginning of each day. This usually consisted of a steady clockwise circuit of the tank about once every 30 seconds. When the framework without any strands of twine was put in this circuiting continued unchecked.

Once the barrier was put in the pattern of movement changed depending on the particular barrier used. Where the barrier was effective the fish started to circuit in the end of the tank to which they were confined at the beginning of the experiment: occasionally individual herring would swim through the barrier as if by "accident". In this case the attractive power of the shoal was always sufficient to cause them to return through the barrier to the main body of fish. Where several fish passed through and the shoal was divided into unequal parts, the smaller group was usually attracted to the larger. Whether a herring, touching the barrier, passed through or not, depended to some extent on the angle of the fish's movement in relation to the barrier. The nearer this was to a right angle, the more likely the fish was to pass through: thus the flight reaction of a fish was usually to increase speed in the same direction.

The most important results were as follows:

1. The effectiveness of the barrier seemed to be independent of the type of material used. Thus white polyfilament nylon drift net twine and white cotton drift net twine were equally effective as barries.

2. Thickness of material was important; thick trawl twine of a given mesh size was much more effective as a barrier than drift net twine. Thus trawl twine with the strands 7.5 cm apart was an almost complete barrier but drift net twine under the same conditions was not.

3. Colour was important. Different colours of drift net twine were used singly or together in the same barrier. The colours which presented the greatest contrast to the grey end walls of the tank *(i.e. black and green)* were most effecitve as barriers. White was least effective. Monofilament nylon, which is almost transparent, acted as a very poor barrier.

4. The mesh size was important. The greater the distance between strands the less effective was the barrier. When the distance between strands approximated to the width or depth of the fish the barrier was effective and no or very few fish passed through it. Thus a distance of 4 cm., using drift net twine, was highly effective against herring 25 cm long but ineffective against herring 12 cm long, for which only distances less than 2.5 cm made effective barriers.

5. While a mesh of a given size was more effective than its horizontal or vertical components alone, there was no consistent evidence of one component being more important than the other.

It is fairly clear then from these results that it is the visibility of the obstacle or barrier which determines how effective it will be, and that visual perception is the main means by which herring avoid obstacles. This was most obvious in the first part of each experiment when the behaviour of the fish without any disturbance was watched. However, given sufficient stimulation in the second part of each experiment the herring was always eventually frightened through even the most effective barriers.

There was no evidence of learning behaviour during the experiments.

2.2 Experiments in Low Light Intensities or Darkness

The experiments under these cond were carried out with a barrier whichl effective in daylight (*i.e.* mesh size or s distance of 4.0 cm for 25 cm fish). In com darkness the fish were found to pass thr barriers which they avoided in daylight. emphasises again the importance of sig obstacle avoidance. On the other hand, he were seen on occasions to be swimming the barrier in darkness and it is possible they were employing a tactile sense.

Observations were made on the cr light intensity for shoaling and obstacle dance. Shoaling began to cease at abou lux in light-adapted fish and at 0.001 l dark-adapted fish. Obstacle avoidance be ineffective at about 0.001 lux in light-ad fish and at a figure lower than this in adapted fish (? 0.0001 lux).

3. DISCUSSION

The results of these experiments t some light on:—

(a) the way in which herring caught in gill nets,

(b) the means by which the ciency of such nets mat increassed.

It seems clear that vision is the important means of perception of "obstacles herring. It is therefore unlikely that captu gill nets is ever likely to be effective in intensities above the critical value of 0.00 unless the water is very turbid, or the n more or less invisible, or the fish are subje some "abnormal" behaviour stimulus. Ev the dark the presence of the net may be visible by phosphorescence from other organ or by the presence of fish which have al been caught. At night, when the light inte falls below a critical level, the herring s rise in the water and break up (and at the time they may begin to feed). They will th swimming at random in the upper water l in which the gill-nets are present. Whil fish will be moving individually at night, will probably be moving in shoals by day an process of capture will differ by day and by n

Our experiments suggest that there are factors which play a major role in determining the process of capture. These are:

(1) The "awareness" of the herring of the nets. This will be determined principally by the visibility of the nets to the herring, but other tactile senses may play a part.

(2) The presence (or absence) of "fright" or "panic" stimuli operating in the vicinity of the nets. The violent movements of a herring already gilled may be an important source of such stimuli.

(3) The orientation of the fish to the nets. Our experiments show that the duration of movement of the herring after contact with the nets, aud therefore whether the fish will be meshed or not, depended on the angle of contact, and on the part of the body with which the contact was made.

(4) The general level of "activity" of the fish.

At present it is not possible to establish the relative importance of these factors, although the experiments indicate the vital importance of the visibility factor, which influences choice of material to be used in net construction. This is of particular importance in gill-netting in clear water in daylight. Further experiments both in the laboratory and the field are planned to determine the origin and possible importance of "flight" or "panic" reactions in the catching process. In particular, attempts will be made to determine the effects of fish already gilled on the reactions of other fish in the vicinity of the nets. This is of importance not only in the elucidation of the capture mechanism, but also to the problem of gear saturation, which affects fishing tactics.

3.14 The Behaviour of Roach *(Rutilis rutilis L.)* in Temperature Gradients in a Large Outdoor Tank

J. S. Alabaster
Ministry of Agriculture, Fisheries & Food, London
and
A. L. Downing
Water Pollution Research Laboratory, Stevenage

0. INTRODUCTION

In Britain there are places, notably near tricity Generating stations, where a rela- y large proportion of a river is used for ng purposes and returned after use to the . The temperature of this water is usually d by 7° or 8°C but the difference in tempera- between the warmest and the coldest water e river itself may exceed these values if, as metimes the case, the amount of cooling r required is greater than the available flow ie river and recirculation of the river water s place. Thus near the outfalls of heated ents and sometimes also near the cooling r intakes, when there is recirculation of river water, very marked temperature ients occur, not only along the length and across the width of the river but, because of the tendency of the warm water to remain at the surface, in the vertical plane too. It is not known what effect such conditions have upon fish; on the one hand heavy mortalities are sometimes attributed to excessively high temperatures and on the other hand fish are said to congregate in the neighbourhood of warm water outlets. Experiments have therefore been started to study the reaction of fish in temperature gradients.

Work of this kind already reported in the literature shows that for many different species there is a definite preferred temperature but, with the exception of Carp (Pitt, Garside and Hepburn, 1956) and Rainbow trout (Garside and Tait, 1958) the authors do not know of any studies on species which occur in Britain.

Where information is available for a species both for temperatures selected in the laboratory and for those at which they are found in the field, there is a fair measure of agreement in the case of fish favouring relatively low temperatures, but for fish living in warmer water the temperatures at which they occur naturally appear to be somewhat lower than those they select in tanks (Ferguson, 1958). It has been suggested that this may be because fish used for laboratory experiments tend to be smaller and younger than natural populations but it may also be connected with the fact that the fish have had only short distances to swim to reach their preferred temperature in laboratory apparatus.

The apparatus used in the present study is larger than any which has been used by other workers so that large individuals can be tested. It will be possible to employ both very shallow and quite steep temperature gradients and also to cause rapid changes in the distribution of temperatures somewhat similar to those caused in rivers by generating stations which operate only for peak load periods. The tank and the ancillary services, including laboratory facilities, have been made available by the Central Electricity Generating Board at the Grove Road Generating Station, St. John's Wood, London.

During the winter of 1957-8 the performance of the apparatus has been determined and some experiments with fish have been made. Since these experiments were made before the methods of operation of the apparatus were developed to a stage at which the experimental conditions could be completely satisfactorily controlled, their results are necessarily of a preliminary nature.

The work with fish has been carried out by the Ministry of Agriculture, Fisheries and Food, and that on the performance of the apparatus by the Water Pollution Research Laboratory.

1. APPARATUS

The apparatus (Fig. 1) consists of a large open concrete tank divided by movable partitions so as to form a winding channel about 152 m. long, 1.3 m. wide and 1.2 m. deep, which is connected to a small heating chamber nearby. In the simplest method of operation wat continuously recirculated through the he chamber where it is raised in temperature then through the channel in which it coo loss of heat to the surroundings. Under con conditions an equilibrium is established so there is a regular gradient in temperature the inlet to the outlet, the positions of w may be interchanged by reversing the flow. main pump used to recirculate liquid H maximum delivery of about 13.6 m^3/hr. lower rates may be obtained by throttling flow with a gate valve. Auxiliary pumps also available to augment this flow or to p water from different parts of the channel.

Steam at a pressure between 275 and cm. Hg. is used to heat the water, the w or part of the flow of steam to the he chamber being controlled if required by m of an automatic valve which closes when temperature of the water attains a sele value. In winter a flow of steam in the re of 230 kg./hr. is required to heat the full flo water to about 35°C.

The temperature of the water at a nu of points is continuously recorded with mer in-steel thermometers and similar thermom housed in a Stevenson's Screen are use measure the wet and dry bulb temperatur the air. For determining water temperatur a point a thermistor is used.

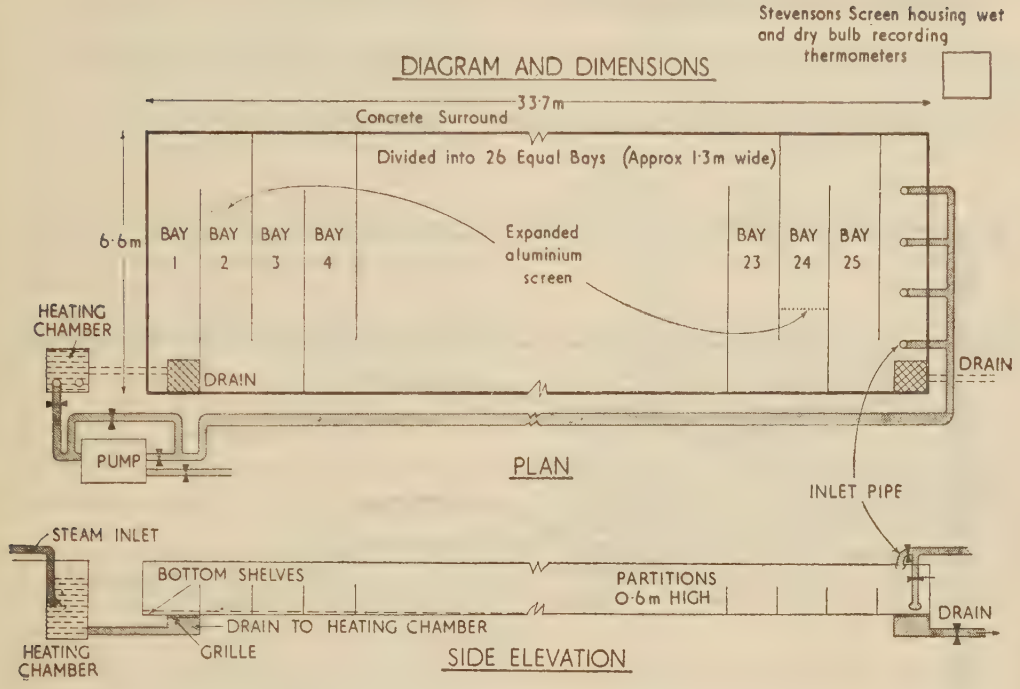
2. PERFORMANCE OF APPARATU

2.1 Preliminary Observations

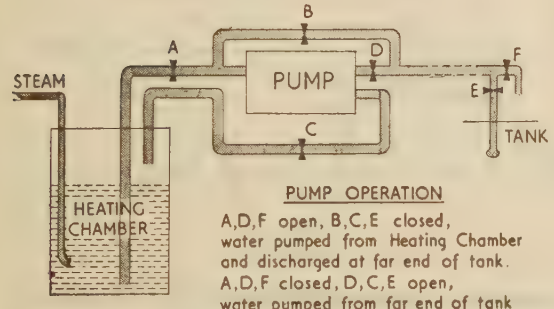
The first trials with the apparatus sisted simply in circulating water through different rates of flow, with different con flows of steam, and recording water and temperatures. At high flows when starting water at the ambient temperature, the temp ture at different points in the channel at rose rapidly as the heated water reached t then remained approximately constant f period about equal to the time of retentio the water in the channel, and then rose f rapidly but by less than on the first occa This continued for about 4 or 5 reten periods, the increases in temperature becon gradually smaller until finally they were detectable. After a time equal to about 4 re tion periods, however, an "equilibrium" reached in which there was an approxima

EXPERIMENTAL INSTALLATION FOR STUDYING EFFECTS OF TEMPERATURE ON FISH

FIG. 1



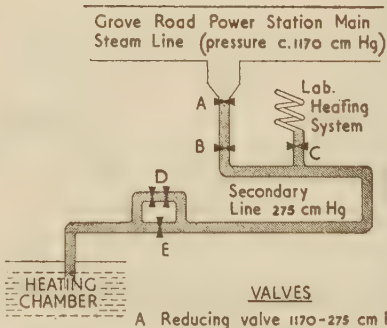
RECIRCULATION SYSTEM



PUMP OPERATION

A,D,F open, B,C,E closed, water pumped from Heating Chamber and discharged at far end of tank.
A,D,F closed, D,C,E open, water pumped from far end of tank into Heating Chamber.

STEAM SUPPLY



VALVES

A Reducing valve 1170–275 cm Hg.
B Safety valve (max. press. 275 cm Hg.)
C Motorised valve controlling Laboratory heating.
D Twin valve controlled by Foxboro–Yoxall Valve.
E Bypass line control valve.

PARTITION DETAILS

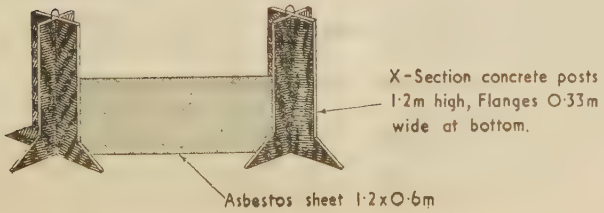
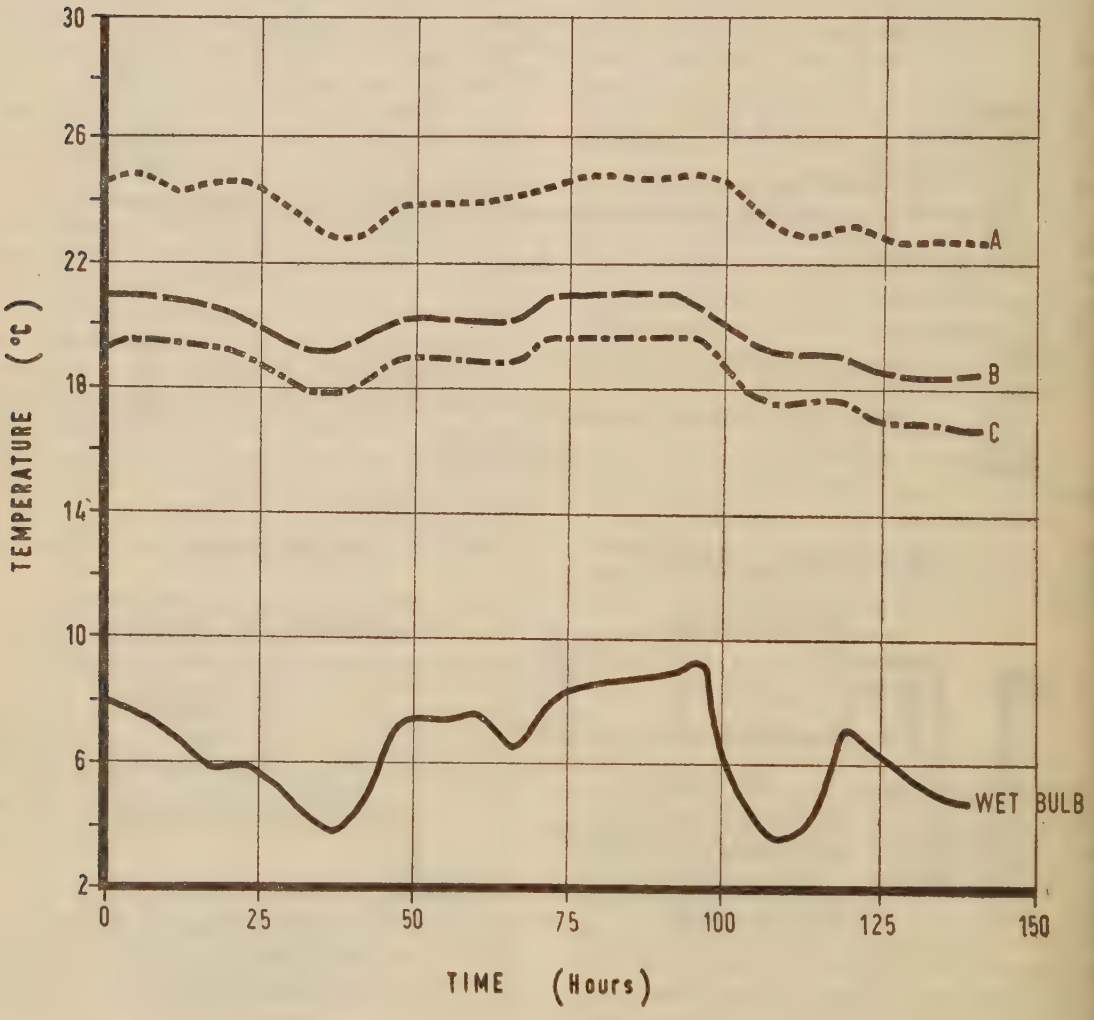


FIG. 2

VARIATION IN TEMPERATURE OF WATER AT THREE POINTS IN THE CHANNEL AND OF THE WET BULB TEMPERATURE OF THE AIR AFTER "EQUILIBRIUM" HAD BEEN ESTABLISHED DURING OPERATION OF THE APPARATUS WITH A CONSTANT FLOW OF WATER AND STEAM



Rate of recirculation of water: 9·5 m^3 per hour.

A: 183 m. from inlet

B: 792 m. from inlet

C: 116 m. from inlet

tant gradient in the channel in the direction w, and a very slight vertical gradient, but hich the temperature at all points tended to uate with the ambient temperature (Fig. 2). behaviour at lower flows was similar except vertical gradients were much more marked. e vertical gradients could however be ly eliminated if required by diffusing air at derate rate through a porous block in the re of each bay. With the maximum flow of r and steam the inflowing water was raised out 20°C. above the ambient temperature an almost linear gradient (Fig. 3) of about 7 degrees was obtained. The gradient eased somewhat with decreasing flow of r, and decreased with decrease in the flow eam and consequently with decrease in the ss temperature above the ambient.

Interpretation of Performance

Clearly one of the main factors governing ormance is the rate at which the water cools flows down the channel. Consider a thin ical section at right angles to the direction ow in which the temperature is maintained tantially uniform by turbulence but which els along the channel without appreciable itudinal mixing. The rate of cooling in this ion will be proportional to the difference een the existing temperature and the tem- ture which it would attain if allowed to e into equilibrium with its surroundings, in rdance with Newton's law. It will also be portional to the surface area across which transfer occurs, and inversely proportional the volume of water. Expressing this braically

$$-d\theta/dt = k\,(A/V)\,(\theta - \theta_E) \quad \ldots\ldots (1)$$

re θ is the temperature of the water at time the equilibrium temperature, A the surface , V the volume, and k the constant of pro- ionality, which is called the cooling coeffi- t. In water flowing in an open channel it is ly that some cooling will occur at the bed of channel, but if this is of thick dense material ow conductivity as in the present case, once ed has been "warmed-up" the rate of cooling kely to be small by comparison with that at the water interface, and as a first approximation ay be neglected. In this case A in Equation becomes the surface area of the water and A/V may be replaced by 1/h, where h is the average depth of the water. Making this substitution and integrating leads to

$$\log_e \left\{ (\theta_2 - \theta_E)/(\theta_1 - \theta_E) \right\} = -kt/h \quad \ldots\ldots (2)$$

$$\text{or} \quad (\theta_2 - \theta_E) = (\theta_1 - \theta_E)e^{-kt/h} \quad \ldots\ldots (3)$$

Then since $t/h = V/(Fh) = wx/F$,

where w is the width and x the distance along the channel, and F is the rate of flow

$$(\theta_2 - \theta_E) = (\theta_1 - \theta_E)\,e^{-kwx/F} \quad \ldots\ldots (4)$$

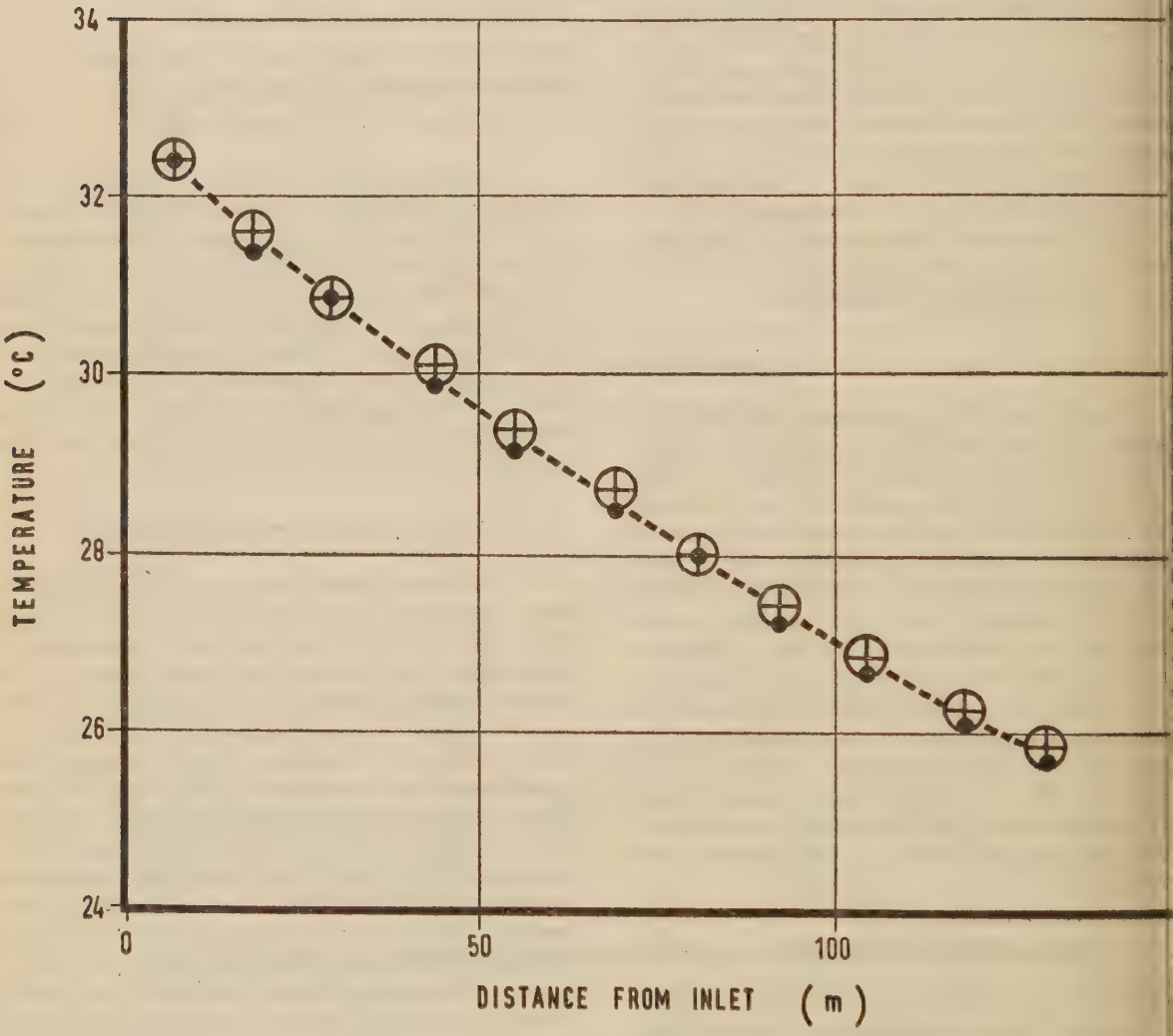
These simple exponential relations describe the form which the gradient in the channel should take, under idealized constant conditions, in terms of its dimensions, the excess temperature, the operating conditions and the cooling coefficient. Provided that the actual conditions are not drastically different from those assumed the gradient may thus be approximately predicted for all conditions for which the cooling coefficient and the excess temperature are known.

2.3 Equilibrium Temperatures

If the ambient temperature and humidity were constant, the water received no heating from solar radiation, and the rate of exchange of heat with the bed was very slow, then in due course heated water would be expected to cool to a temperature close to the wet-bulb temperature of the air. However, during daylight the equilibrium temperature will tend to be higher than the wet-bulb temperature because of heating by solar radiation. Formulae have been developed by which, with the aid of appropriate meteorological data (cloud cover, angle of inclination of the sun, etc.) it is possible to estimate the equilibrium temperatures under such conditions. They may also be estimated empirically from experimental data for the particular system involved by determining, by trial-and-error, the value which gives a linear variation of $\log_e (\theta - \theta_E)$ against time or distance (in accordance with Equation 2), preferably for a range of fairly small values of $(\theta - \theta_E)$ for which the variation in the logarithms is large. Yet another method is to record the water temperature for the system when no artificial heating is applied, and to determine how this is related to the prevailing air temperatures. This latter method was used to estimate the temperature of the Thames

FIG. 3

DISTRIBUTION OF TEMPERATURE IN CHANNEL DURING OPERATION AT MAXIMUM FLOW OF WATER AND CONSTANT FLOW OF STEAM



ary in the absence of heated discharges meson, Hall and Preddy, 1957) and from from three stations it was concluded that verage equilibrium temperature was appro- tely equal to 0.5°C plus 1.11 times the emperature (in °C) (Gameson, Gibbs and ett, 1959). Though it has not yet been blished whether this relation would also hold the experimental channel, it seems quite eivable that it might do so. In the mean- e however, it has been found that sufficiently rate predictions for experiments lasting e than a day may be made by assuming the librium temperature to be equal to the wet- temperature, providing as is usually the that the excess temperatures are fairly high.

Cooling Coefficients

The cooling coefficient was estimated the data obtained in the preliminary trials lotting the temperature at different points he channel and the wet-bulb temperature nst time after "equilibrium" had been blished, interpolating on these graphs to find excess temperature of a given body of water uming piston-type flow) as it flowed past erent points in the channel, the retention od between them being calculated from the sured flow and the dimensions of the nel, and substitution of the data in Equation to calculate k. Data obtained during the t for periods when the ambient temperature reasonably constant were used in pre- nce to other data to minimize errors in the mated excess temperatures.

It will be seen from Equation (1) that the ensions of k are those of velocity and the l units chosen to express it are those of hr. The values obtained from the prelimina- experiments range between 1.5 and 3.7 with verage of about 2.5 cm/hr. and it is interest- that these are of the same order as the mated average value for a river, 2.49 cm/hr meson, Gibbs and Barrett, 1959), and an estuary, 3.7 cm/hr. (Gameson, Hall and ddy, 1957). Insufficient evidence was obtained ssess the effect of depth, but the closeness of values for the river, the channel and the ary, the depths of which were considerably erent, suggest that it is not likly to be very e. The data from the preliminary tests cated a decrease in the coefficient with decreasing flow but this was to some extent nullified by a later experiment in which the average value of the cooling coefficient in stagnant water was found to be 2.5 cm/hr. It seems likely therefore that the variations may be due as much to other factors, possibly wind velocity for instance, as to flow. In Fig. 4 are shown the types of gradient which are to be expected in the channel under different operating conditions with constant flow from end to end. It will be seen that large gradients are to be expected only at low flows, with high excess temperatures, but that under these conditions the gradients are markedly non-uniform. It can also be seen that the uncertainty in the value of the cooling coefficient causes an appreciable uncertainty in the value of the predicted gradient, but nevertheless it has been found so far that by taking the cooling coefficient equal to the mean value 2.5 cm/hr, for all conditions, sufficiently accurate predictions for experimental purposes are obtained.

2.5 Excess Temperatures

Suppose that water initially at a temperature, θ_E, in equilibrium with its surroundings, is recirculating with a flow, F_W, and that the flow of steam to the heating chamber is F_S. If water and steam are uniformly mixed, all the steam is condensed, there are no heat losses and the volume of water condensed from steam is small by comparison with the total volume, then the water entering the channel will be raised to a temperature θ_{H1} given by

$$F_W(\theta_{H1}-\theta_E)=F_S(Q-\theta_{H1}) \quad \ldots\ldots\ldots (5)$$

where $(Q-\theta_{H1})$ is the heat given up per unit weight of steam condensed and cooled to θ_{H1}, the value of which is a function of its temperature and pressure, and can be found with the aid of steam tables. Thus

$$\theta_{H1}=F_S(Q+F_W\theta_E)/(F_W+F_S) \quad \ldots\ldots\ldots (6)$$

Water entering the channel at a temperature θ_{H1} will cool to θ_{C1} by the time it reaches the outlet where by Equation (3)

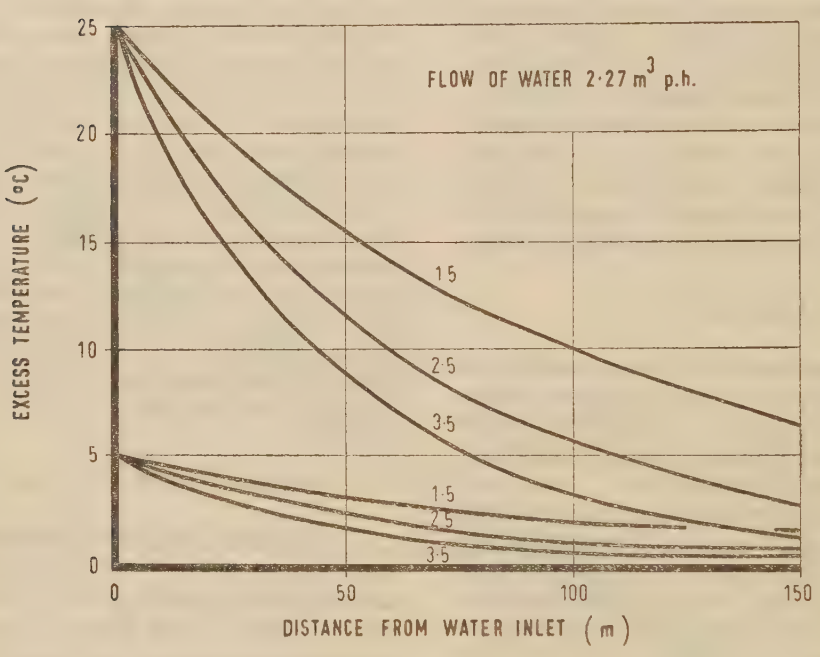
$$\theta_{C1}-\theta_E=(\theta_{H1}-\theta_E)\,e^{-kt/h} \quad \ldots\ldots\ldots (7)$$

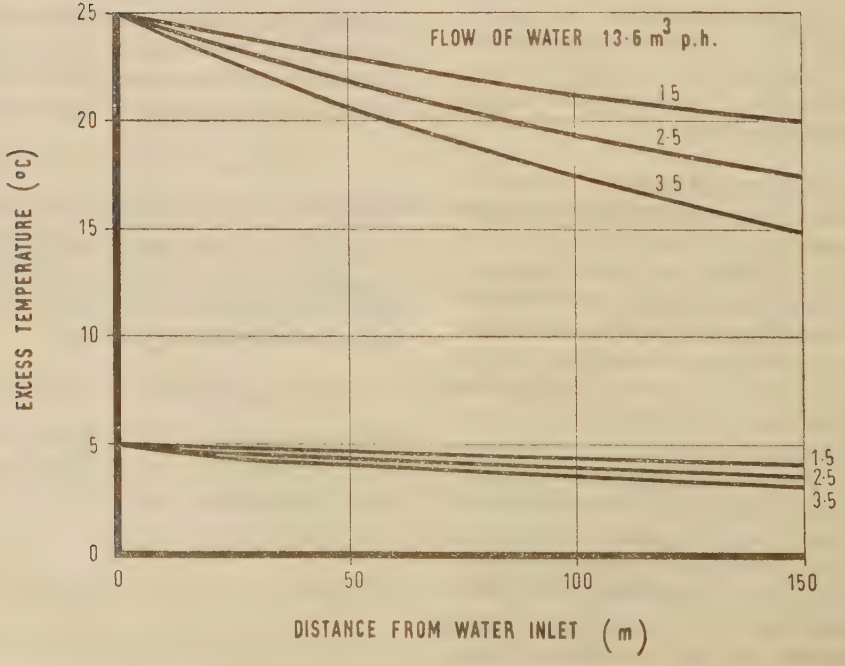
This water will then be reheated to θ_{H2} where

$$\theta_{H2}=(F_SQ+F_W\theta_{C1})/(F_W+F_S) \quad \ldots\ldots\ldots (8)$$

FIG. 4

TYPES OF GRADIENT ATTAINABLE IN EXPERIMENTAL CHANNEL WITH A CONSTANT FLOW OF WATER FROM END TO END. ASSUMED VALUE OF COOLING COEFFICIENT SHEWN AGAINST EACH CURVE.





substituting from Equation (7)

$$= F_S Q + F_W \left\{ (\theta_{HI} - \theta_E)\ e^{-kt/h} + \theta_A \right\}$$
$$/ (F_W + F_S) \quad \ldots\ldots (9)$$

as $F_S \ll F_W$ Equations (6 and (9) may be itten

$$= \theta_E + r \quad \ldots\ldots (10)$$

$$= \theta_E + r + re^{-kt/h} \quad \ldots\ldots (11)$$

re $r = F_S Q/(F_W + F_S) \simeq F_S Q/F_W$
similarly

$$= \theta_E + r + re^{-kt/h} + r(e^{-kt/h})^2 \quad \ldots\ldots (12)$$

erally since the terms following θ_E are in metric progression

$$= \theta_E + r \left\{ 1 - (e^{-kt/h})^n \right\}$$
$$/ (1 - e^{-kt/h}) \quad \ldots\ldots (13)$$

the final temperature, θ_F, attained by the wing water is given by

$$= \theta_E + \operatorname{Lt}_{n \to \infty} r \left\{ 1 - (e^{-kt/h})^n \right\}$$
$$/ (1 - e^{-kt/h}) \quad \ldots\ldots (14)$$

is by

$$= \theta_E + r / (1 - e^{-kt/h}) \quad \ldots\ldots (15)$$

Equations (13) and (15) thus relate the rating conditions to the predicted tempera- in the channel at any time and at final ilibrium.

It will be seen from Equation (13) that e r is positive and $e^{-kt/h}$ is positive and less 1 1, the temperature of water entering the nnel will increase by successively decreasing ements at intervals of one retention period. vever, if the steam supply is automatically trolled to heat the water to a fixed selected perature then this stepwise build-up will se when this temperature is reached. This , of course, be achieved almost immediately r starting if the steam supply available is e enough. In Fig. 5a are shown the pre- ed variations in temperature at two points he channel for a relatively low flow of steam ch is controlled when the temperature ches 10°C, and for a constant ambient tem- ature. This is to be compared with Fig. 5b in which are shown the observed variations for similar conditions but with normal fluctuations in ambient temperature. It is seen that the observed temperatures are somewhat different and their variations are less sudden and more irregular than the predicted values partly owing to the fluctuations in ambient temperature and partly to longitudinal mixing in the channel.

2.6 Effect of Variations in Ambient Temperature

If the system were in equilibrium, the flow of steam constant, and the heating chamber temperature not controlled, a rapid increase in ambient temperature to a new constant value would cause the temperature of the inflowing water to change to a new value in accordance with Equation (13) but the gradient, though affected initially, would tend ultimately to return to the same value as before. It appears that this tendency toward a constant gradient under conditions of constant steam flow is largely realized in practice, even though the ambient temperature is rarely constant for sufficiently long for a true equilibrium to be reached. As has already been mentioned a kind of pseudo-equilibrium is attained in which the gradient changes relatively little with the changes in ambient temperature and the temperature of the water varies directly with them as shown in Fig. 2. From graphs of the deviations of the temperature of the water from its average value plotted against the corresponding deviations from the mean ambient temperature, it appears that there is an approximately linear correlation between the two. From the slopes of lines fitted by eye to the data it is concluded that a change of 1°C in ambient temperature causes a change of about 0.45°C in the temperature of the water.

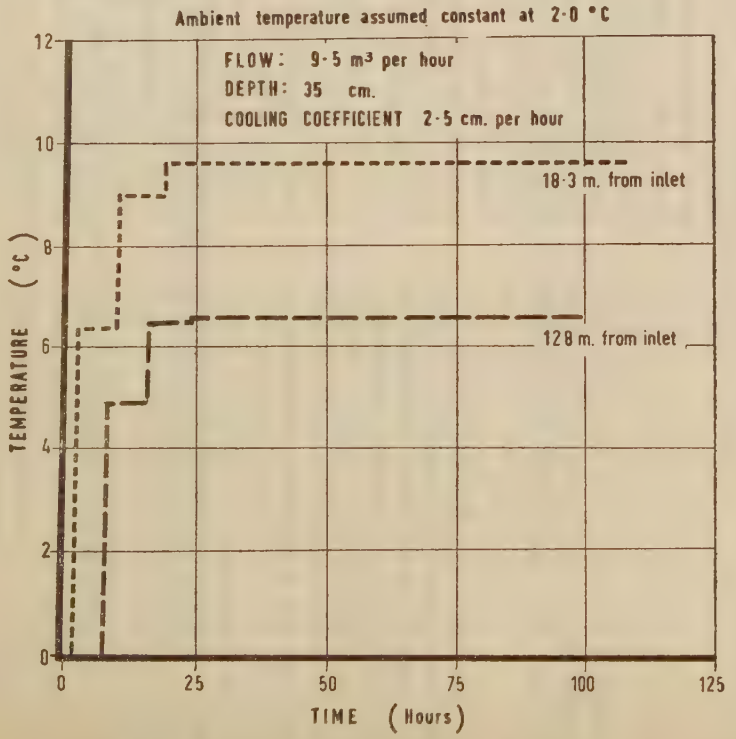
On the other hand if the temperature of the heating chamber is controlled to a constant value then variation in the ambient temperature merely causes the gradient to vary. An example of this is shown in Fig. 5b in which it is seen that after an approximate equilibrium is established with the ambient temperature at about 4° to 5° C, a sudden increase in ambient temperature to about 10.5°C caused the gradient also to decrease rapidly. In this particular case control of the heating chamber to 10°C as was intended could not be maintained since the ambient temperature eventually exceeded this value.

FIG. 5

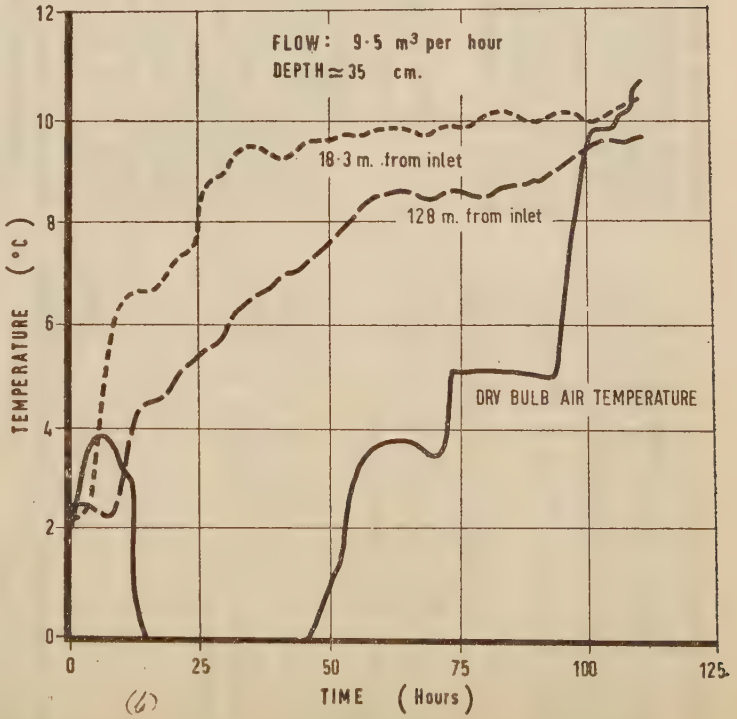
CALCULATED AND OBSERVED VARIATIONS OF TEMPERATURE OF WATER AT TWO POINTS IN THE CHANNEL WHEN HEATING FROM COLD.

STEAM FLOW CONTROLLER SET TO GIVE FINAL HEATING CHAMBER TEMPERATURE OF 10 °C

CALCULATED



OBSERVED



(6)

Alternative Temperature Distributions

Only a limited range of gradients is attainable by straightforward operation of the apparatus with the water flowing right through the channel from inlet to outlet. However, with a suitable combination of flows and pumps a considerable variety of temperature distributions can be formed. The method for selecting the required distribution may be illustrated by considering what is required to produce a nearly linear variation in temperature along the channel, assuming that say 5 pumps are available. Suppose that a flow, F_A, of heated water with an excess temperature θ_A is injected at a point A at one end of the channel and that flows F_B, F_C, F_D, F_E are withdrawn at points B, C, D, E, downstream at distances X_B from A, and X_C, X_D, X_E apart respectively (Fig. 6). This water is all returned to the heating chamber where it is reheated to θ_A and returned to point A. Assuming constant conditions the excess temperatures ultimately attained at B, C, D and E will be given by

$$\theta_B = \theta_A e^{-k_{AB} w x_B / F_A} \quad \ldots\ldots (16)$$

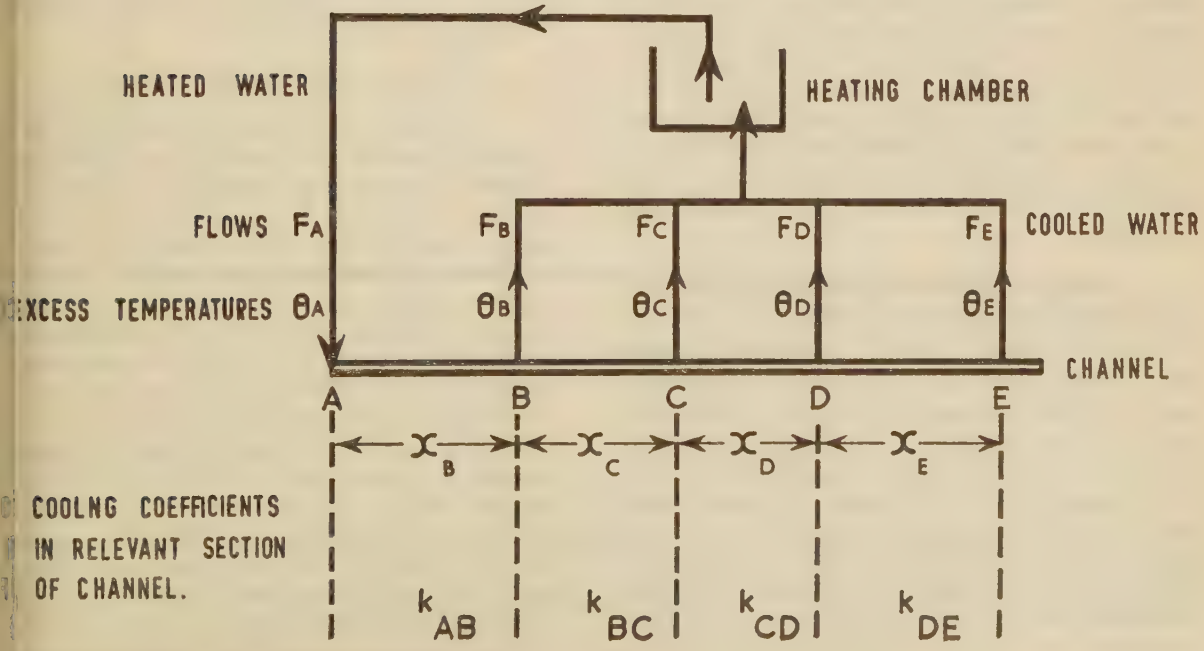
$$\theta_C = \theta_B e^{-k_{BC} w x_C / (F_C + F_D + F_E)} \quad \ldots\ldots (17)$$

$$\theta_D = \theta_C e^{-k_{CD} w x_D / (F_D + F_E)} \quad \ldots\ldots (18)$$

$$\theta_E = \theta_D e^{-k_{DE} w x_E / F_E} \quad \ldots\ldots (19)$$

FIG. 6

RATES OF FLOW AND POSITIONS OF PUMPS ASSUMED FOR ILLUSTRATION OF METHOD OF FORMING STEEPER AND MORE UNIFORM TEMPERATURE GRADIENTS IN THE CHANNEL



where k_{AB}, k_{BC}, k_{CD} and k_{DE} are the cooling coefficients between the stations. (Note that in this context θ_E does not represent the equilibrium temperature). In principle the best distribution of pumps and flows could be calculated from the above equations by trial and error but it is sufficient in practice to assume the pumps to be spaced at equal intervals and to calculate the flows which would give equal intervals of temperature between the various points. The condition for this to occur, which is easily derived from the above equations, is that

$$(1/E_{AB}) + E_{BC} = (1/E_{BC}) + E_{CD} = (1/E_{CD}) + E_{DE} = 2 \quad (20)$$

where E with the appropriate subscript represents the relevant exponential function from Equations 1 to 4. Now if the temperature range required is a fraction x of θ_A it must be arranged that

$$\theta_A - \theta_B = x\theta_A/4 \quad (21)$$

that is, that

$$1 - E_{AB} = x/4 \quad (22)$$

The required flows may then be calculated from Equations 20 and 22.

It may be noted that there is no point in taking $x = 1$ since this would involve the water cooling to the equilibrium temperature and in theory this could occur only in an infinite period of retention in the section DE, and lead to an exponential variation of temperature in this section. To obtain a linear variation it is better to be content with a final temperature about 0.5° C. above the equilibrium temperature in which case if $\theta_A = 10$°C., for example, we should take $x = 0.95$.

In Fig. 7 are shown the calculated flows and the resulting predicted temperature distribution for a value of θ_A=20°C., when the required temperature variation is $0.96\theta_A$ over a 152 meter section of the channel; the cooling coefficient has been assumed to take a constant value of 2.5 cm./hour. It is seen that the predicted variation in temperature in the channel is nearly linear over about ¾ of its length but that there is some departure from linearity in the last section. This predicted deviation from linearity could probably be made smaller by small alterations in the position and flow of the pumps at 114 and 152 m. from the inlet or by using a further pump at some point between them. However it is thought that in practice longitudinal mixing will generally tend to smooth out such deviations and make the adjustments outlined above unnecessary. Also shown in Fig. 7 are the predicted and observed temperature distributions using only 3 pumps, spaced at different intervals, and returning cooled water. The two curves are by no means coincident but there is a sufficient measure of agreement to support the validity of the method.

2.8 Fluctuating Conditions

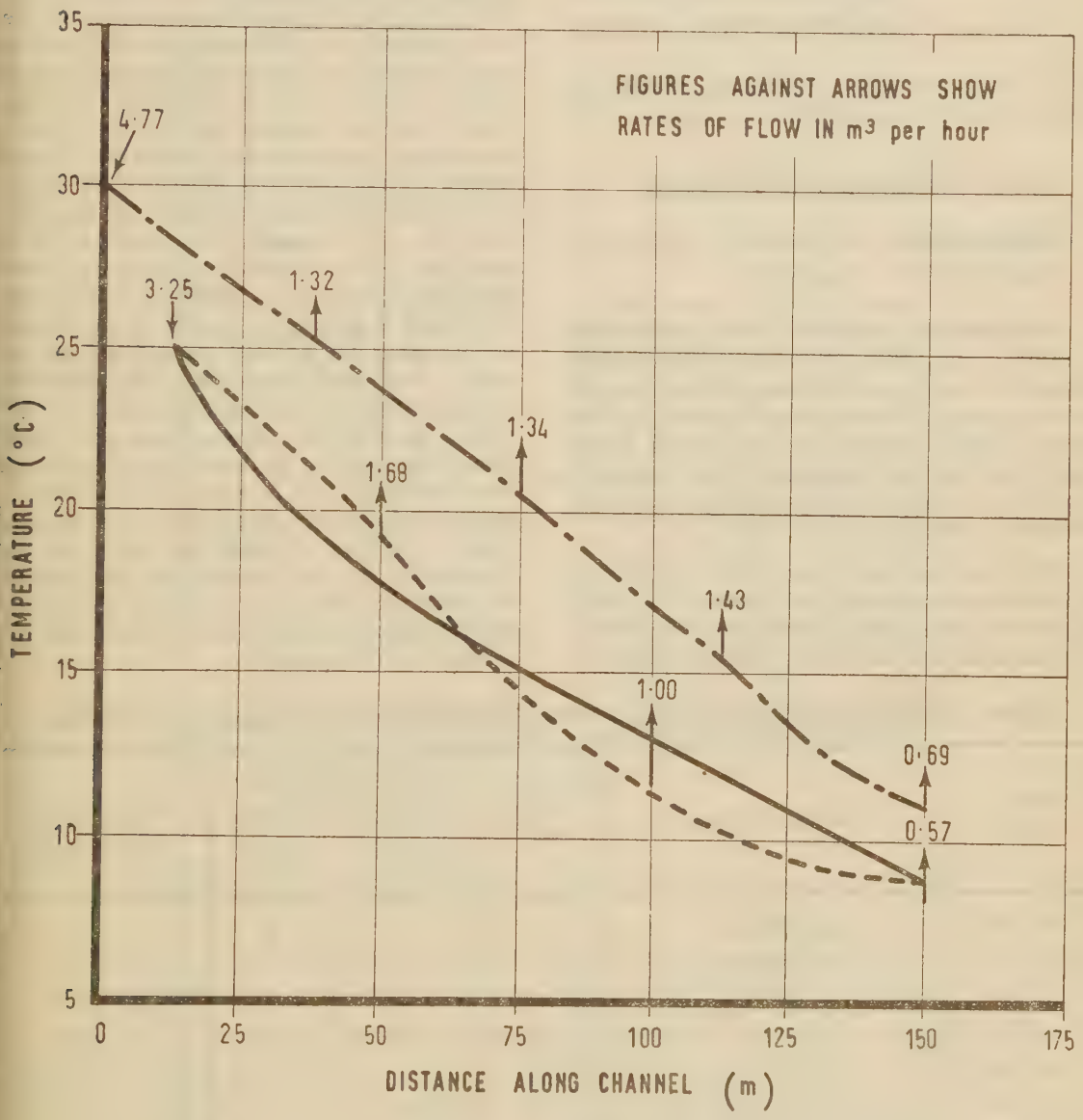
The response of fish to irregular temperature fluctuations is also of interest in the present investigation. Such conditions can be produced by varying the flow of the water or steam intermittently. For instance the temperature distribution may be quickly altered by simply reversing the flow, or a band of cold water may be passed down the channel by turning off the steam supply, closing the outlet, pumping a quantity of cold water at the inlet and then switching on the flow of water and steam again. A band of hot water may be passed down the tank by switching on the heating for a short period when the tank contains cold water. The disadvantage of this method, however, is that the hot water inevitably cools and loses heat by mixing but it is hoped eventually to devise techniques to overcome this.

2.9 Concentration Gradients

It may be mentioned in passing that the apparatus may also be used for investigating the effects of concentration gradients. Of particular interest is the effect of gradients of dissolved oxygen since in some circumstances these can occur as a result of temperature gradients because of the variation in the solubility of oxygen with temperature. Such gradients can be studied independently by adding a deoxygenating reagent (such as sodium sulphite plus a small concentration of cobalt chloride) to the recirculating unheated water. Since the rate of change of the oxygen concentration is proportional to the oxygen deficit, the variation in concentration with time or position follows the same relations as were developed for the variations in temperature. Thus if the water is initially saturated with oxygen and the flow of sodium sulphite adjusted to cause an initial oxygen deficit

FIG. 7

PREDICTED AND OBSERVED TEMPERATURE GRADIENTS IN CHANNEL WHEN RECIRCULATING WATER FROM SEVERAL POINTS AT DIFFERENT FLOWS



PREDICTED; ASSUMED WET-BULB TEMPERATURE 10 °C; COOLING COEFFICIENT 2·5 cm. per hou

PREDICTED; ASSUMED WET-BULB TEMPERATURE 8·4°C; COOLING COEFFICIENT 2·5 cm. per hou

OBSERVED; AVERAGE WET-BULB TEMPERATURE OVER PRECEDING 2 DAYS 8·4 °C

the water entering the channel, then the oxygen deficit at the inlet end of the channel at the end of n-1 retention periods of duration, t, would be given (by analogy with Equation (13)) by

$$D_n = D\left\{1-(e^{-ft/h})^n\right\}/(1-e^{-ft/h}) \quad \ldots\ldots (23)$$

where f is the exchange coefficient (Gameson, Truesdale and Downing, 1955) for oxygen.

3. EXPERIMENTS WITH FISH

3.1 Distribution of Roach with no Temperature Gradient

Observations with fish in the tank were first made when there was no temperature gradient, both with and without recirculation of the water, since it was possible that in the absence of any temperature differences some particular location in the tank might be favoured by the fish and also that their behaviour might be affected by the direction of flow.

The tank was set up as shown in Fig. 1, filled with water to a depth of about 30 cm and supplied with a flow of air through the diffusers. Roach about 15 cm long which had been kept in stock tanks at a temperature of about 9°C v introduced into the tank on November 20th, 1 one batch of 100 in bay 8 and another sin batch in bay 18. The water was not recircul and there was no detectable gradient of temp ture along the tank. Observations on the were started the following day and the si shoal into which they had formed was ea visible from the side of the tank. Occasion it split into two or more groups but these c usually be seen without difficulty. The di bution of the fish was measured by recor the position of individual shoals at quarter h intervals over a period of about eight h each day. The observations made on Nover 21st are shown in Fig. 8A from which it app that there is no strong tendency for the sh to be observed at any particular part of tank. A similar picture (Fig. 8B) was obta a few days later at a similar temperature (7. when, during the observations and over preceding period, the water was recirculate the maximum rate of about 13.6 m³/hr. results for several successive days are sum rised in Table 1 in which the tendency for observations to be made at one or other en the tank has been expressed as the numb bays the median shoal position is displaced the centre of the tank.

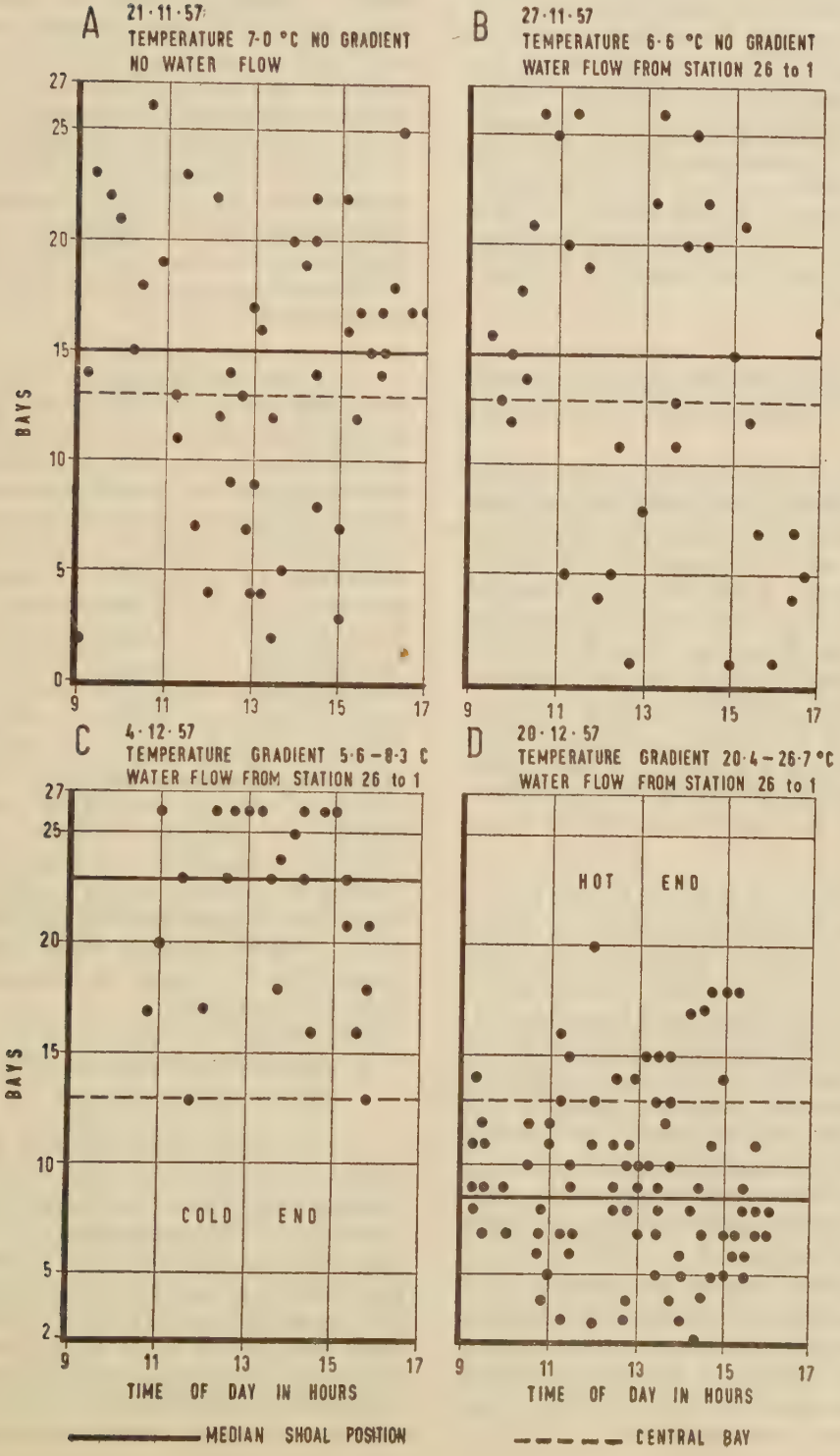
Table. 1. Behaviour of roach in the channel in the absence of a temperature gradient

Date (1957)	Direction of flow	Temperature (°C)	Displacement of median shoal position from central bay		Minimum rate o swimming (bays/hour)
			Towards Bay 1	Towards Bay 26	
Nov. 21	none	7.0		2	27
Nov. 25	Towards Bay 1	5.2	4		8.5
,, 26	,,	5.6	4		5.8
,, 27	,,	6.6	0	0	28.8
,, 28	,,	7.3		2	25.0
,, 29	,,	8.3	4		20.5
Dec. 2	,,	3.0	11		0

It can be seen that the displacement is not very marked except in the last case when the temperature was about 3°C. On this occasion the fish remained all day in a single shoal within a small area of bay 2 and this inactivity was in strong contrast to what obtained at higher temperatures, as is illustrated by the minimum r of swimming which have been included in table. These have been calculated from quarter hourly observations, selecting only obtained when the fish were in a single s and assuming that they travelled by the sho

FIG. 8

DISTRIBUTION OF ROACH SHOALS IN THE CHANNEL



route from one observed position to the next. There appears to be an approximate relation between temperature and minimum rate of swimming and this may help to explain the anomalous result at 3° C. It is possible that the fish simply happened to be in bay 2 when the temperature dropped and were "trapped" by the cold. Other possibilities are that at low temperatures fish tend to remain in deep water (the tank is slightly deeper at bay 1 than elsewhere) or that fish swim down current when there is a fall in temperature. Insufficient data have yet been collected to enable us to decide between these possibilities.

3.2 Distribution of Roach in Longitudinal Temperature Gradients

Observations of the behaviour of roach in temperature gradients were made at the same depth of water and under the same conditions of aeration and with the same fish as in the control experiments. Examples of two kinds of result which have been obtained with a temperature gradient are shown in Figs. 8C and D. Both were obtained from water flowing from bay 26 to bay 1; in one case the gradient was from 8.3 to 5.6°C and in the other from 20.4 to 26.7°C. In the former there is a strong tendency for the shoals to be found in the warmer water, whereas in the other the fish seem to prefer the lower temperature.

In the case of the results in Fig. 8D, in which there was a marked splitting up of the shoals into small groups making a relatively large number of observations available, an examination (Holt, 1958) showed that they conform to a restricted normal distribution. It would thus be possible to define the distribution in terms of a mean and standard deviation and to substitute the temperature which corresponded to these values in the channel. However, in many other cases only a few shoals formed and so relatively few observations were available. Because of this and also because of the restricted and variable nature of the temperature gradients, the median shoal position was simply determined by inspection and the displacement of this median from the central bay in the channel used as a measure of the attraction for the fish of the warmest or coldest water available.

The rest of the results are summarise Table 2 and it is seen that they fall in on other of the two types illustrated in Figs and D. Where the maximum temperature less than 10°C. only small gradients achieved, the largest being 2 7°C., and in group of results the most marked displace of the median shoal position from the ce bay was found when the gradient was betv 1° and 2.7°C. Where the minimum tempera was greater than 10°C. the maximum tem ature was always 5°C. higher but on no occa was the distribution of the fish towards one of the tank so marked as it had been at the lo temperatures.

These results suggested that given a restricted choice the fish would have chos temperature somewhere between 10° and 1 and this was confirmed in later tests in Janu Gradients in which the difference between highest and lowest temperatures was 15° to 2 were established and it was found that observations of shoal positions were not crow at one or other end of the channel. The me shoal position was determined and the temp ture to which it corresponded interpolated the temperature records at bays 3, 7, 12, 18 22 and this was taken as the tempera "selected" by the fish. The results (Tabl show that, as before, reversing the directio flow does not alter materially the tempera selected but also show a slight tendency for selected temperature to increase with t During the previous weeks the lowest temp ture in the channel was on several occasion high as 20°C. so that there had been s opportunity for the fish to become acclimat to high temperatures.

3.3 Effect of Time upon Temperat Selected by Roach

A further opportunity of measuring effect of time on the reaction of roach temperature gradient was taken when a grad from about 25°C. to a temperature within a degrees of ambient (5° to 10°C.) was mainta for nearly two weeks during February. The for this experiment were first put into the some time before these conditions were fi obtained; 200 roach, about 15 cm. long, introduced about a month beforehand, 20 ro about 30 cm. long, were added a week later,

Table 2. Behaviour of roach in a temperature gradient

Date (1957)	Direction of flow	Average temperature (°C.)		Temperature gradient between Bays 4 and 22 (°C.)	Displacement of median shoal position from central bay	
		Bay 4	Bay 22		Towards Bay 1	Towards Bay 26
Dec. 4	Towards Bay 1	5.6	8.3	2.7		10*
Dec. 5	do	7.6	9.8	2.2		10*
Dec. 6	do	8.9	10.0	1.1		12*
Dec. 9	do	8.9	10.5	1.6		12*
Dec. 10	do 26	9.4	8.2	1.2	10	
Dec. 11	do	9.9	8.9	1.0	4	
Dec. 12	do	10.0	9.5	0.5	2	
Dec. 13	do	10.0	9.1	0.9		0
Dec. 14**	do	8.3	7.6	0.7	7	
Dec. 16	do	5.1	2.8	2.3	10	
Dec. 16	do 1	6.0	7.7	1.7		10
Dec. 17	do	11.5	17.8	6.3		5
Dec. 18	do	16.6	23.5	6.9	5	
Dec. 19	do	17.9	24.7	6.8	3	
Dec. 20	do	20.4	26.7	6.3	5	
Dec. 23	do	19.0	24.3	5.3	3	
Dec. 24	do	19.7	25.1	5.4	5	
Dec. 27	do	19.5	24.7	5.2	5	
Dec. 30	do	17.3	22.9	5.6	9	

*Only one observation made
**Screens not yet put in Bays 2 and 24.

Table 3. The temperature selected by roach in a temperature gradient

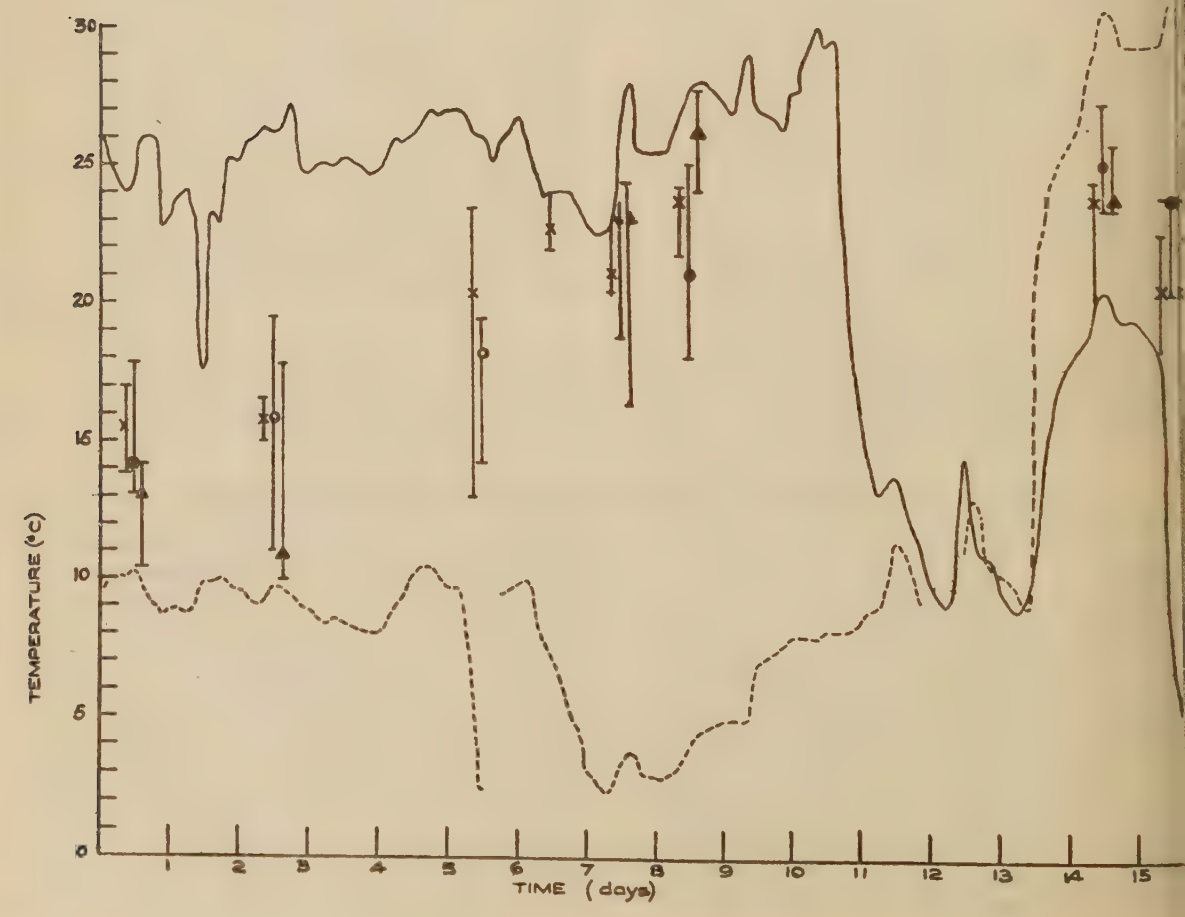
Date (1958)	Direction of flow	Temperature (°C.)		Temperature selected (°C.)
		Bay 3	Bay 22	
Jan. 6	Towards Bay 26	23.4	10.0	15.0
Jan. 7	do 1	14.3	21.0	16.0
Jan. 8	do 1	15.6		16.0
Jan. 9	do 1	16.0	21.0	18.6

several hundred, 5-cm. roach were put in only a few days before the experiment was started. The temperature during this preliminary period varied considerably and was often as high as 20° C.

The same experimental procedure as before was followed once the gradient had been established and in addition to the continuous measurement of temperature at different parts of the tank a thermistor was used, usually once a day, to measure the temperature in each alternate bay. The observations of the shoal positions did not appear to be distributed normally and so the median and range of shoal posi measured for each day and the temperature to which they corresponded interpolated graphs of the temperature profile along the Results are shown in Fig. 9.

There is a considerable range of tem tures within which the fish are observed on one day and although this never includes entire range of temperature available, it amount to 8° or 9°C. in some cases. There also day-to-day differences in the rang temperatures selected but there does appear a tendency for the selected temperatur

FIG. 9 TEMPERATURES SELECTED BY ROACH IN A TEMPERATURE GRADIENT


TEMPERATURE AT BAY 3 (°C.)
" " " 22 "
THE TEMPERATURE FOR EACH MEDIAN POSITION OF SHOALS IS THE AVERAGE OVER THE PERI OF OBSERVATION IN ANY ONE DAY
MEDIAN POSITION OF SHOALS OF LARGE ROACH
" " " " " MEDIUM "
" " " " " SMALL "
TEMPERATURE RANGE TRAVERSED BY SHOALS DURING OBSERVATION PERIOD
TEMPERATURE (°C)
TIME (days)

ease with time. The temperature corres-ling to the median shoal position was ini-y about 14° C. and increased to about 23°C. a week. It was still at this value when the ient was re-established in the reverse ction after a period of two days when the perature had fallen to about 10°C.

Generally fish shoals were composed of of one predominating size and although the tions they occupied in the tank were rent, there were no marked or consistent rences between shoals of different sized fish the whole period.

Observations in Irregular Temperature Gradients

In addition to experiments where condi-s were kept as constant as possible for long ods, others were carried out in which the ilitions were intentionally changed during course of the day. They were undertaken ly to investigate the reaction of fish to rapidly ging conditions (as might occur in rivers iving heated discharges) and partly to see ther the temperature selected by the fish was ificantly affected by the position they pied in the tank, or by the fact that the nest water available was always in the ream direction.

One experiment was carried out with 200 ium sized roach in water no warmer than to see whether they would select the warmest er available by swimming down current. A ient from 9 to 7°C. was set up from bay 26 bay 1 and then the flow of water was ped. Cold water was added to the tank at 1 and the warmer water was pushed back rds bay 26. The temperature along the th of the tank was measured several times ng a day with a thermistor and the fish shoal tions observed every quarter of an hour. results (Fig. 10) show that the fish moved ne down stream end of the tank and kept y from the coldest water.

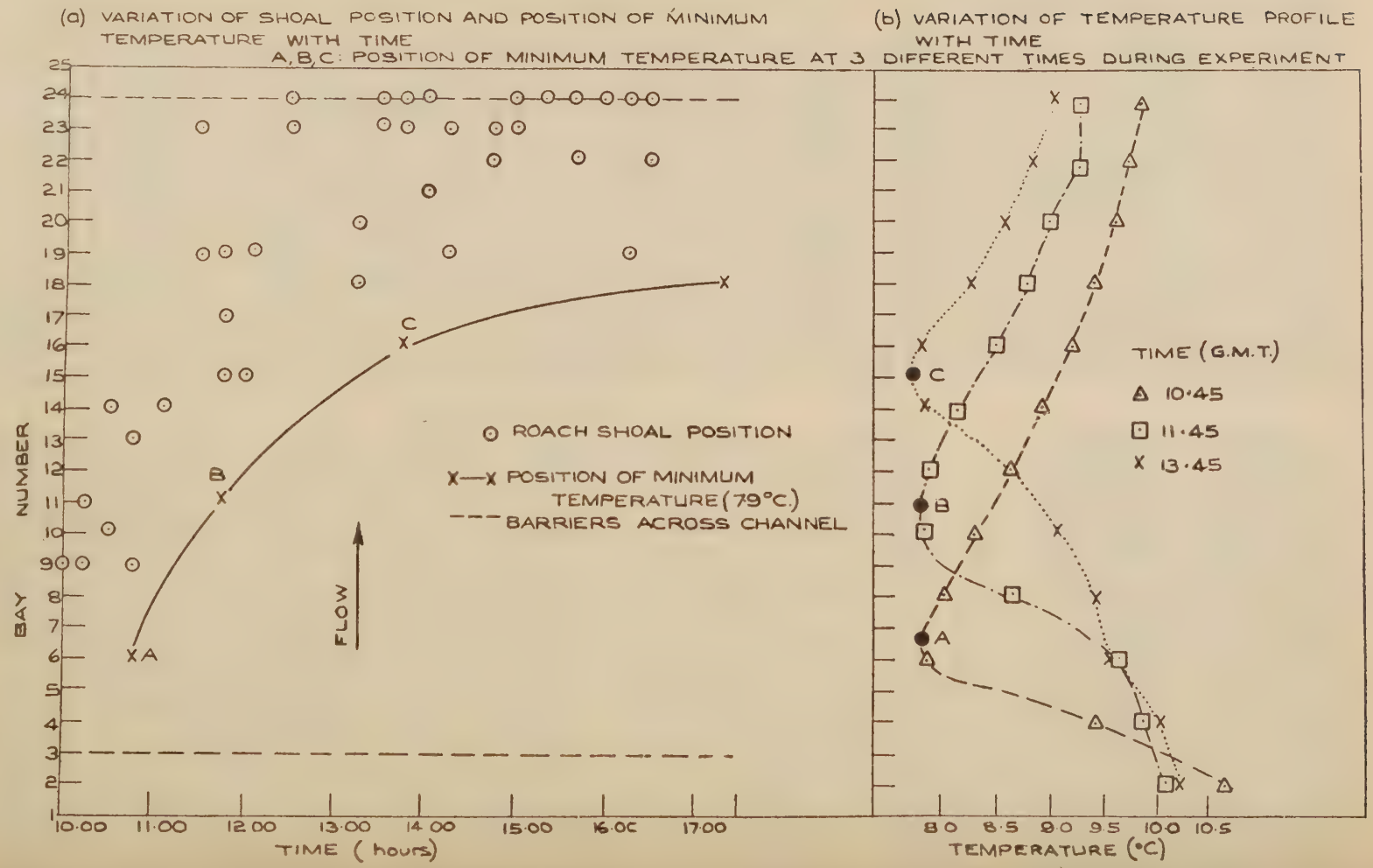
However, roach did not invariably avoid water in an experiment of this kind where total gradient was only a few degrees igrade. In one experiment 20 large roach put into the channel and a gradient from 13°C. established by recirculating the water injecting a controlled quantity of steam into heating chamber. The fish which remained single shoal, swam to and remained at the warmest end of the channel. The steam supply was shut off for about an hour and a band of cold water passed down the tank. Almost as soon as the temperature fell at the end of the channel where the fish were congregating, the fish showed a marked increase in activity and ranged over almost the entire length of the channel. The shoal was watched almost continously and a record of its movements is shown in Fig. 11. The fish did not avoid the cold water to the same extent as the smaller roach had done in earlier tests and they appeared to be stimulated to such activity that they overshot the rather narrow band of warm water each time they came to it. As soon as the steam supply was turned on again and the fish had swum to the warm end of the tank, there was a marked reduction in their activity and they remained near the barrier again.

Another experiment was carried out at a somewhat higher temperature and with steeper gradients, and a more definite distribution of observations was obtained. The flow was initially from bay 15 to bay 1, the water being static in the other half of the tank. The temperature at bay 15 was about 23°C. and there was a fall of temperature of only a few degrees towards bay 1 but the temperature fell steeply to about 10°C. towards bay 26. Large and medium sized roach were present and their shoal positions were observed at 15 minute intervals. After about an hour the flow was reversed by pumping water out from bay 26 and returning it back to bay 1; as no heating was used a band of warm water, sandwiched between two areas of cold water, moved along the tank towards bay 26. The temperature was measured hourly in each alternate bay with a thermistor and continuous thermographs were available at fixed points in the channel. The results are shown in Fig. 12. The fish moved in a down-stream direction and tended to remain in the warmest water available to them.

4. CONCLUSIONS

From the experience gained during operation of the experimental unit under a variety of conditions it is concluded that it will be possible to produce with it, and control satisfactorily, most of the temperature distributions likely to be required for a general investigation of the response of fish to temperature gradients in flowing water.

FIG 10 REACTION OF MEDIUM SIZED ROACH TO A FRONT OF COLD WATER



REACTION OF A SHOAL OF 20 LARGE ROACH TO FLUCTUATING TEMPERATURE CONDITIONS IN A TEMPERATURE GRADIENT

FIG.11

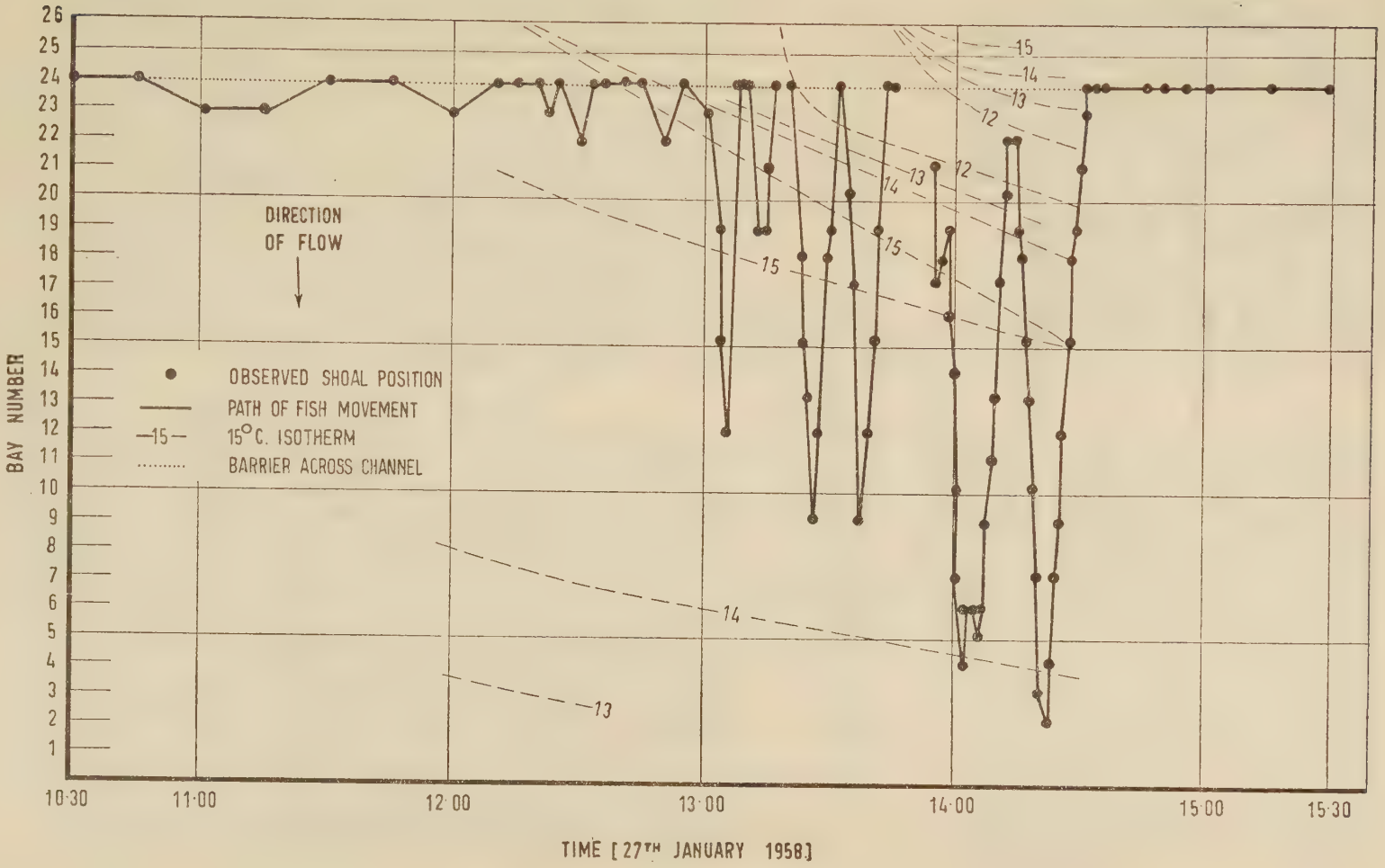
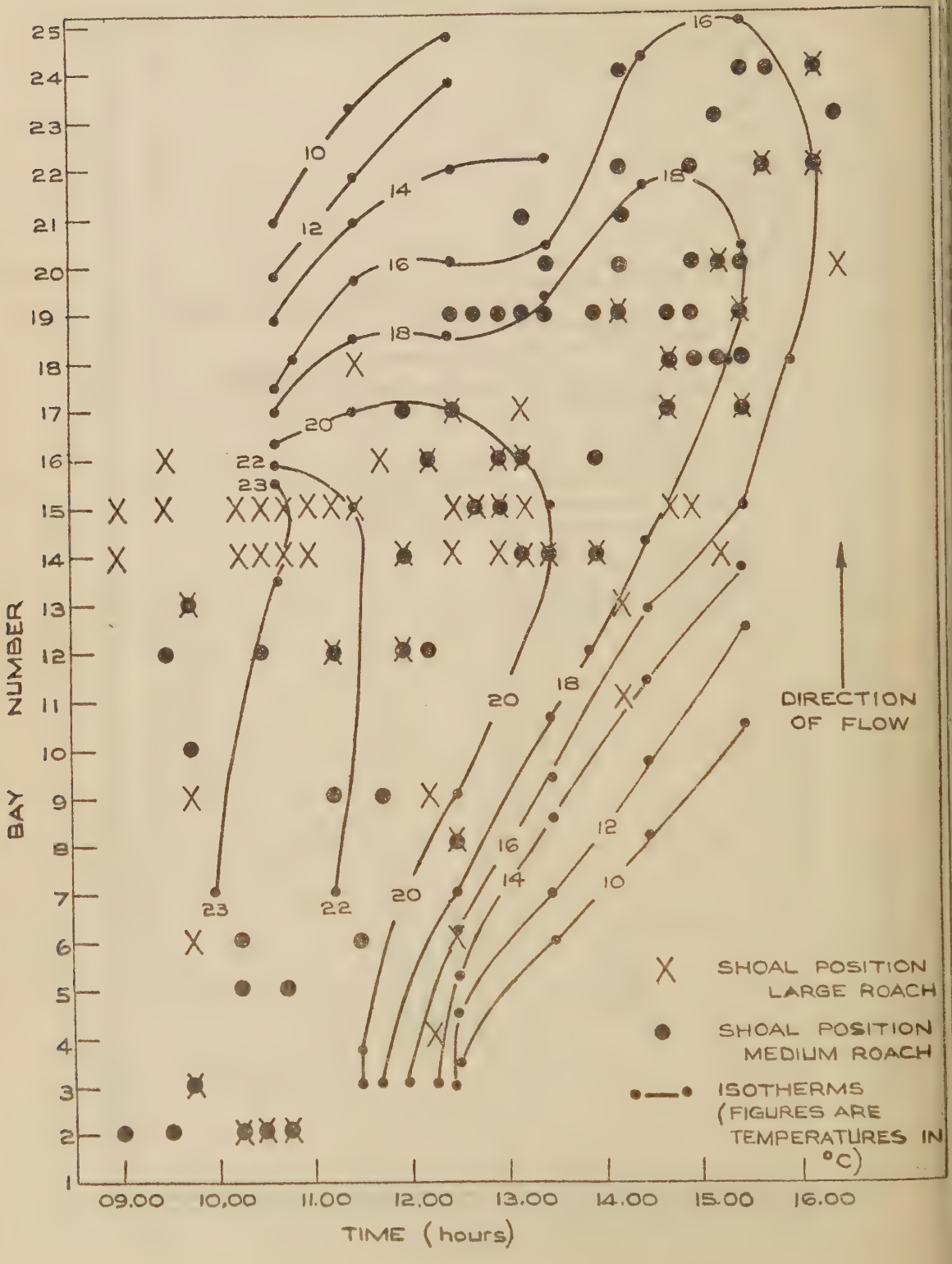


FIG 12 POSITION OF ROACH SHOALS UNDER CONDITIONS OF RAPIDLY CHANGING TEMPERATURE



From the experiments which have been de so far it is not possible to specify precisely temperature which roach select when offered hoice in a gradient but it does appear that vided the choice is wide enough they will ntually select a temperature of about 23° or C. over a period of one or two weeks, nough shoals of fish will occasionally be found water as high as about 27°C.

Experiments in temperature conditions ich change fairly quickly show that the ection of current and the position which the occupy in the tank do not necessarily in- ence the apparent selection of temperature, eed under certain conditions the fish selecting rm water can be made to move down stream remain in it.

There appears to be no marked difference in the reaction of roach of different sizes when tested together in longitudinal temperature gradients.

ACKNOWLEDGEMENTS

The authors are grateful to the Central Electricity Generating Board for providing facilities for carrying out the work described.

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3.15 A Preliminary Note on a Multiple Apparatus Recording the Activity of Fish in Semi-Wild Conditions

D. R. Swift *

It has long been known that fish living in nperate climates grow at rates that differ m one season of the year to another; but at time the present work was begun it was still t known with any certainty how this growth- e cycle varied during the year. The first ults obtained, published in 1955, and the ults of work carried out since then show arly that brown trout in Great Britain, ether in the hatchery or wild, and whether ture or immature, follow the same growth-rate ttern during a year. This pattern can be nmarised as follows: low growth-rate during nter, high rate in spring and often (but not ways) in autumn, marked depression of growth e in midsummer.

The existence of this growth-rate rhythm ving been demonstrated, work is now pro- eding to ascertain the cause of the rhythm d in particular of the very interesting midsum- r depression. This work is at present pro- eding along two lines: firstly, the growth-rate being measured of fish living at temperatures d day-lengths held constant at different levels; condly seasonal variations, if any, in the activity of brown trout living in semi-wild conditions are being investigated. It is this second line of work which is reported on here. The decision to investigate the muscular activity of fish was made for the following reasons. Firstly there is no information, so far as the author is aware, on the amount of movement a fish makes in a particular period. Secondly seasonal changes in energy use in muscular activity could have important influence on fish growth-rate.

While observations of the amount of movement performed by a fish in an ordinary aquarium would be of some value, such results could not be taken to be representative of the changes that may occur in the wild. Since obviously it is impossible to obtain detailed information of this kind from wild fish in wild conditions, an attempt has been made to approach the wild conditions as near as possible while still being able to record the movements of the fish.

The fish used in this work are all wild brown trout from Lake Windermere and all are about 17 cm long. Each fish is held separately in a cage sunk onto the bed of the lake and each

* Freshwater Biological Association, The Ferry House, Ambleside, Westmorland, England.

cage is 8 feet long by 2 feet square. The cage is made of wood and covered in netting of appropriate mesh size to keep the fish in and to allow passage to invertebrate food animals. The fish are given no artificial food and feed entirely on organisms reaching them through the netting. Equally spaced along the length of the cage are three pairs of electrodes. These electrodes form part of a resistance bridge system which is thrown out of balance every time the fish passes between a pair of electrodes. This passage is recorded by a pen on a continuous recorder and a counter summates the number of times per day the fish passes between the three pairs of electrodes in its cage. In this way it is hoped to get both the diurnal rhythm from the recor and by plotting daily totals to get the seasc variations in total activity.

At the time of writing this report c a single cage pilot apparatus was working, a definite diurnal and seasonal rhythm in activity of the fish was already apparent. I obvious that with an apparatus of this sor will be possible to correlate activity accurat with variations in the features of the envir ment, such as in temperature and light.

The apparatus has been designed built by Mr. W.H. Moore of the Freshwa Biological Association, Windermere Laborat

3.2 Field Research

3.21 Fish Behaviour and the Planktonic Environment: the Role of Field Observations

R. S. Glover *

The following extracts are from the Prospectus for the Symposium:

(page 1) "The analysis of the relations between behaviour and its environmental determinants would permit development of techniques of prediction of distribution from observation of environmental elements".

(page 3) ".... what measurement of environmental factors determining behaviour need be made to permit .... some prediction of fish behaviour and hence its consequences to the dynamics of fish populations.

The recent increase in research on fish behaviour is a logical, and most welcome, addition to the techniques of fishery biology. Valuable results may be expected from laboratory experiments but the experimentalist must draw on the experience of the field ecologist if there is not to be a wastage of time and effort.

Firstly, the experimentalist can make many short cuts if he is told which factors are most likely to be limiting to the distribution, shoaling, feeding, spawning and survival of f The field worker must be prepared to g advice on such questions.

Secondly, the results of laboratory exp ments must be tested in the field. The dang of drawing conclusions from isolated crui are well-known and the tests will usually invo quantitative studies of the fish and its envir ment based on observations collected over a l period of years. Considerable time will be sav therefore, if records of fisheries and environm are made in a manner which is likely to be use in testing the experimentalists' hypotheses.

It is impossible to forecast all the ki of field observations which will be required certain basic information can be collected a systematic manner. Indeed, a variety of su records and collections are already stand practice; for instance, one may expect to f records of fluctuations in many fisheries, terms of catch per unit-effort, and of the spec and age-composition.

Simple observations of the physical a chemical environment are often availab although the choice of parameters may o

* Scottish Marine Biological Association, Oceanographic Laboratory, Edinburgh.

ething to expediency. For example, it is y to record temperature and salinity; to these sphates and oxygen determinations are some- es added. Because of the importance of eorology there are usually frequent records barometric pressure, rainfall, and wind ngth and direction.

There are no comparable standardised ervations of the biological environment and, many aspects of the biological picture, this navoidable. It is, for instance, difficult to ord fluctuations in the population of a fish dator which is not itself the subject of a com- cial fishery. It should be possible, however, ecord fluctuations in the plankton and there many reasons for supposing that such ervations would be valuable in studies of fish aviour. To name three such reasons:

(1) Phytoplankton is at the beginning of the chain of organic production in the sea.

(2) Plankton is the food of many fish.

(3) Plankton may indicate subtle environmental changes which cannot always be detected by simple measurements of, say, temperature and salinity.

This last point has been emphasized by a nber of workers; see, for example, Fraser 39, p. 33) and Abramova (1956, p. 69).

If long-term observations are to be studied quantitative sense, it is essential to standar- the techniques of collection and treatment. ndardisation is universal in recording such ors as temperature, salinity and wind-strength it is notable that an increasing proportion hese observations is made from commercial sels and shore stations. Indeed, it is relevant onsider the extent to which research vessels uld be used in routine sampling of this kind. value of a research ship lies in the opportu- which it provides to adjust a programme in rdance with changes in the character of the ections. But, for long-term quantitative lies, nothing is more frustrating than the introduced by *ad hoc* changes in objective, rse and technique aboard research ships. s is not to argue that research ships are uitable for this kind of routine work but it s suggest that alternatives should be con- red.

It is now becoming common practice to supply thermometers and water samplers to commercial ships, and further assistance can be obtained from naval vessels. Gear used from such ships must be simple to operate by untrained personnel and its use should not interfere with the normal activities of the ship.

For sampling plankton from commercial vessels, the Hardy Continuous Plankton Recorder and the Plankton Indicator are the only instruments which have been put to the test over a long period of years. The Continuous Recorder has been described by Hardy (1939); Rae (1952) has described the technique of analysis of the samples. Single-and multi-depth models of the Plankton Indicator were described by Glover (1953). These instruments are in use in many parts of the world but their main application is in the surveys carried out from the Scottish Marine Biological Association's laboratory at Edinburgh; most of the results have been published in the "Bulletins of Marine Ecology" which can be obtained from that laboratory.

Briefly, the Continuous Plankton Recorder is towed by commercial passenger ships, freighters and Ocean Weather Ships. It is normally used to sample at a depth of 10 m and the plankton is collected on a continuous moving band of silk, providing a record of the changing composition and abundance of the plankton along the ship's route. The Indicator is towed, for about 1½ miles, at a depth of 8 m, behind drift-net fishing vessels as they steam to or from the fishing grounds. The plankton is collected on a small disc of silk which can be returned to the laboratory for analysis, providing a picture of the animate environment of the herrings which are the subject of a commercial fishery. Both samplers are used at the normal cruising speed of the towing ships and they are easily handled at sea by untrained personnel.

Before proceeding to a very brief illustration of the kind of results obtained from these samplers, it is necessary to emphasize that their use requires a philosophy different from that of classic planktology where the objectives are usually specific and localised.

Continuous Recorder collections may be compared with an anthropological survey conducted from a moving railway train. By watching the towns and country-side through which the

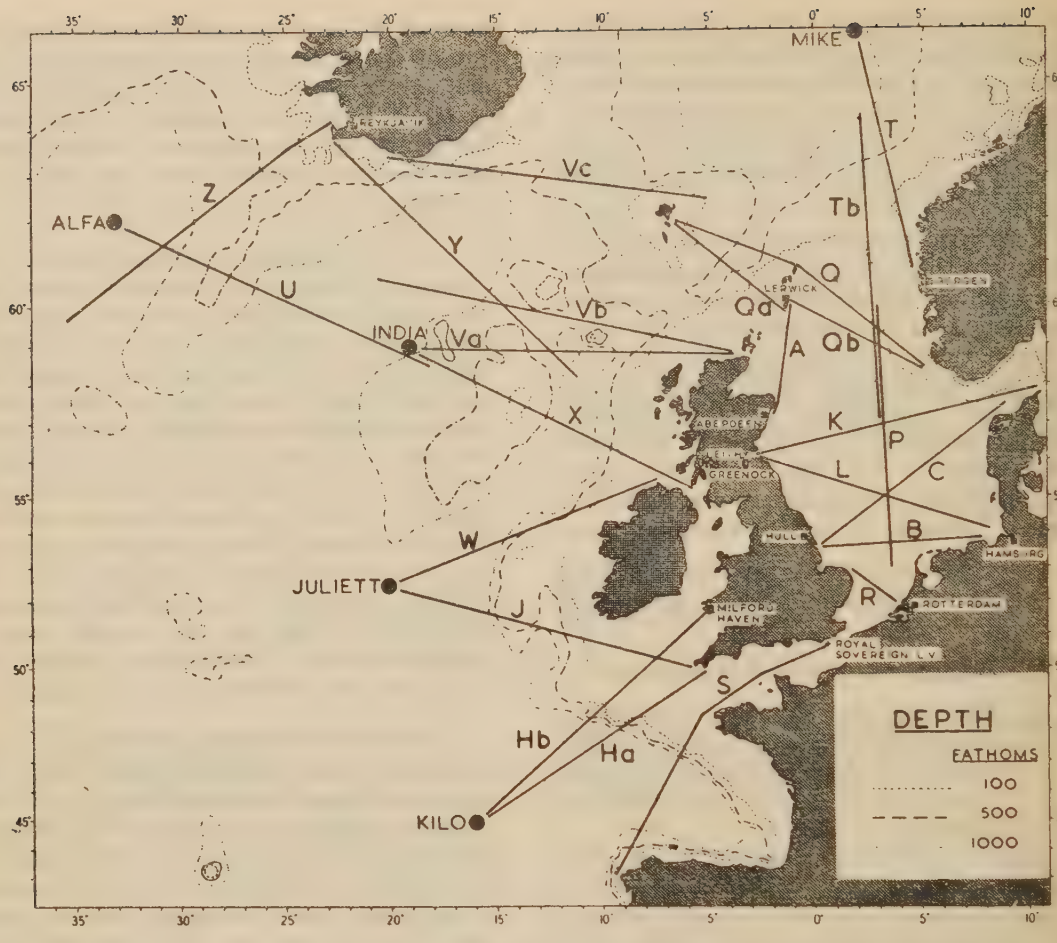

Figure 1

Code letters identify the routes sampled monthly by the Continuous Plankton Recorders for the Oceanographic Laboratory, Edinburgh. International names identify the Weather Ship Stations, (large dots).

train travelled, a passenger could make deductions about the way of life of the people living near the railway line, and these would be supplemented by an inspection of the manners and dress of the passengers who joined the train at each station. But it would be unreasonable to expect to observe intimate family or courtship relationships from observations in a railway train and there would be very little or no information about medical science or religious customs. Similarly, the Recorder survey cannot supply answers to every intimate and detailed biological question but it can supply a wealth of background information which, possibly, can be obtained in no other way.

The value of these instruments lies in their collection of plankton at a constant depth, on fixed routes, at regular intervals of throughout the year and the maintenance of regime over a long period of time. Fig. 1 sh the routes along which Recorders are towe monthly intervals, in the Edinburgh sur This survey was started in 1931 by Sir Al Hardy, at the University College of Hull; objective is to sample the plankton of the C nental Shelf fishing grounds and of the ne bouring oceanic waters.

The Recorder and Indicator collec are used in a variety of studies of the ecolo plankton but most of the work falls into on more of the following categories. It should stressed that there is nothing unique about list except for the advantages which result the use of a standardised technique.

1. *Charting the distribution* of individual species of plankton and, from this:

2. *Definition of the "average" distribution* in terms of time, space and abundance, leading to:

3. *Definition of the "average" species-composition of communities*, so that:

4. *Fluctuations in community composition* can be used to infer environmental change. This is an extension of the idea of using planktonic species as indicators of water movement (see Russell, 1936). The standardization of the technique for many years enables:

5. *The expression of fluctuations in quantitative terms* which can be compared with the "average".

6. *Charting the spawning areas* of benthic organisms and of fish by studying the distribution and dispersal of planktonic eggs and larvae. Frequent sampling permits definitions of the season and duration of spawning. Frequent sampling also allows:

7. *The study of the changing distribution* of individual planktonic species, providing an opportunity to determine whether physical transport, spawning, predation or "metabolic" mortality are the limiting factors in distribution.

The results have been applied to studies ishery problems; for example, the comparison romach contents of herrings with the avail- plankton in the sea, providing a measure of ction in feeding. Multidepth Indicators been used (from research ships) to provide cture of the vertical distribution of plankton elation to the distribution of herring shoals. kers in the U.S.A. and Canada have used the rder to study the dispersal of fish larvae spawning centres. It will be useful, how-, to provide a few brief examples.

My colleagues G.T.D. Henderson, G.A. inson and J.M. Colebrook have provided the erial for Figure 2 which shows charts of rage distribution". The upper charts show distribution of larvae of two fish; *Gadus assou* (Blue Whiting) is not fished commer- y but *Gadus virens* (Saithe) is taken by trawlers. The abundant population of *G. poutassou* in this area was not suspected until the Recorder survey was extended into the Atlantic in 1948; the larvae have appeared every year but only in the months of April and May (Henderson 1957). A striking feature of the charts is the restriction of *G. poutassou* to the west of the Continental Slope (shown by the 100-fathom contour) whilst *G. virens* only occurred over the shallow Shelf to the east of the contour.

The same sharp boundary is apparent (Figure 2) in the distribution of the diatom, *Thalassiothrix logissima* (west of the contour), and the copepod, *Centropages hamatus* (east). The distributions of these species reflect the inflow of mixed oceanic and coastal water into the northern North Sea; *Thalassiothrix* by the intrusion of a tongue into the North Sea, and *Centropages* by an apparent retreat from the south-flowing stream.

Glover (1957) has studied the effect of this inflow of mixed water into the North Sea. Samples collected by fisherman using the Plankton Indicator revealed a striking change in the species-composition of the plankton community over the herring fishing grounds; neritic species, which were abundant during 1947-1950, were gradually replaced by species characteristic of the mixture of oceanic and Atlantic coastal water. (The change is illustrated by Glover, 1957, Text-fig. 11). The increased mixed water inflow was contemporary with a southerly shift of the herring fishing and spawning grounds, with increased length of the herrings and with an abundance of young fish in the catches. It seems unlikely that these changes were the result of a direct feeding effect; it is more probable that the shoaling habits of the herrings and the strength of the recruit brood were dependent on an environmental change which was indicated by the changing community balance of the plankton.

Mr. A. Saville, of the Marine Laboratory, Aberdeen, has also studied the changing plankton community in relation to fishery fluctuations. I am grateful to him for the data from which Figure 3 (A and B) was prepared. Saville (1958) examined the routine Hensen net hauls taken, by the research vessels of the Aberdeen laboratory, from the haddock spawning grounds of the northern North Sea. He calculated the

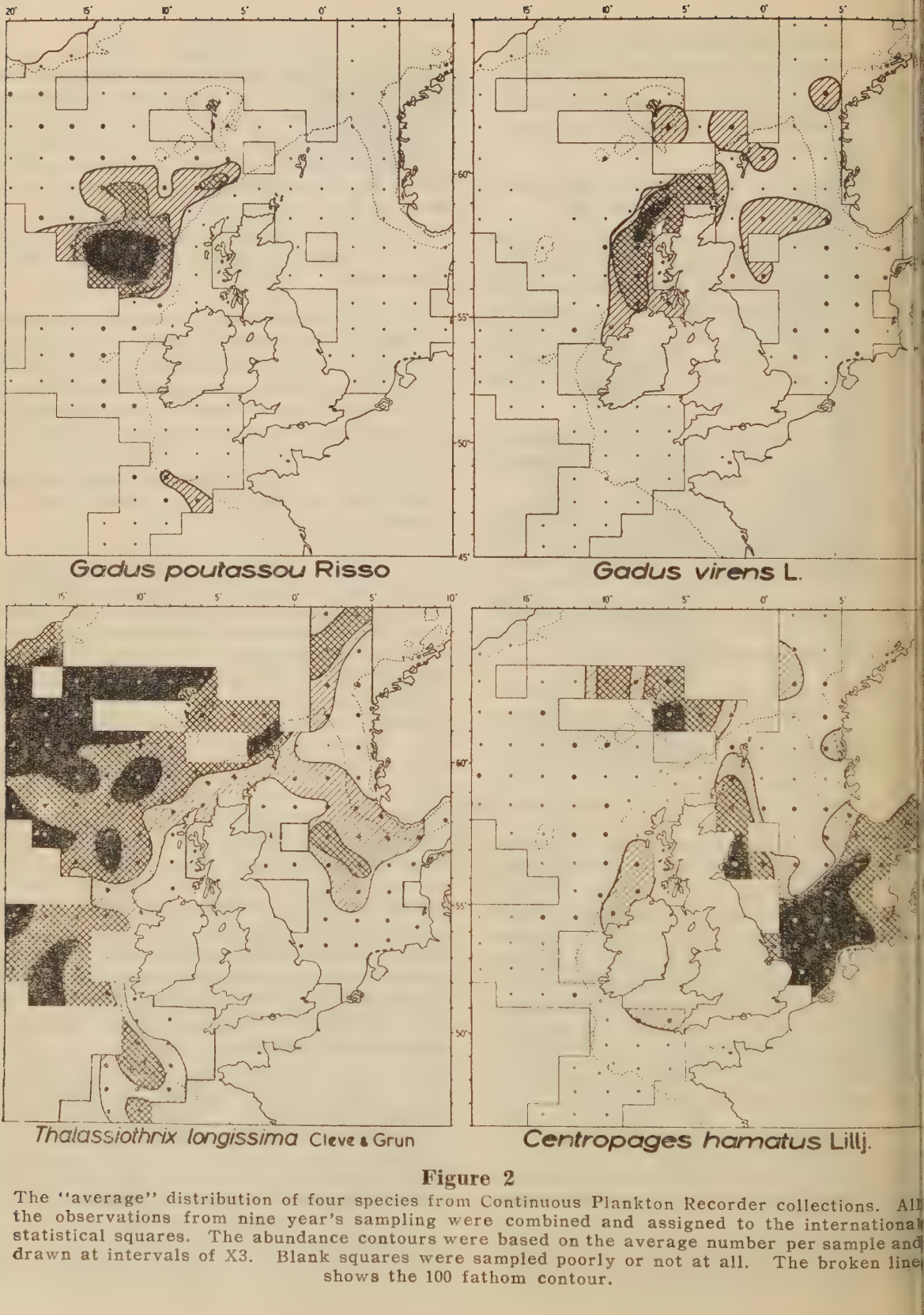

Figure 2

The "average" distribution of four species from Continuous Plankton Recorder collections. All the observations from nine year's sampling were combined and assigned to the international statistical squares. The abundance contours were based on the average number per sample and drawn at intervals of X3. Blank squares were sampled poorly or not at all. The broken line shows the 100 fathom contour.

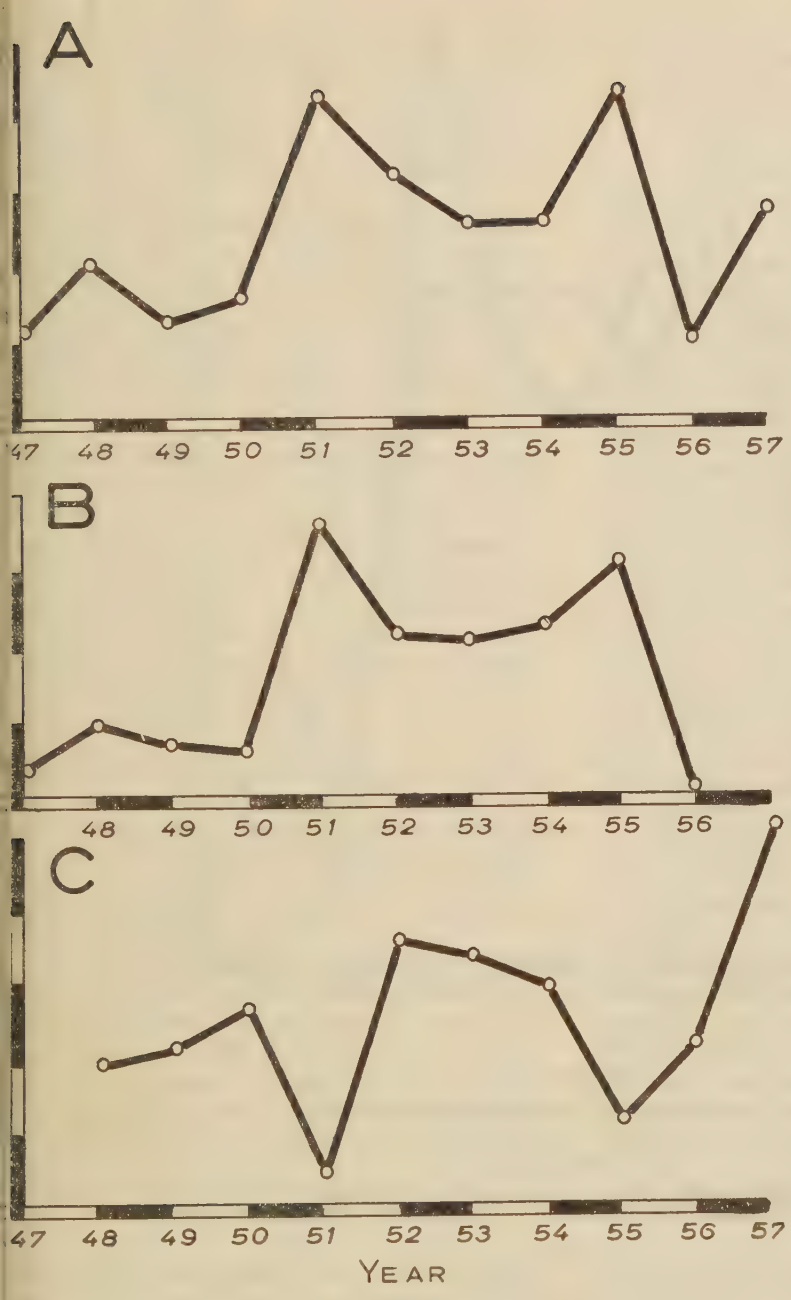

Figure 3

Haddock and plankton in the Northern North Sea.

he percentage of the haddock spawning area which was free of xtonic indicators of neritic or oceanic water (from Saville, 1958).

addock brood strength; the scale is in arbitrary units of abundance n Saville, 1958).

ne abundance of *Calanus finmarchicus*, stages V and VI, in the Conti- s Plankton Recorder collections. The scale is a logarithmic mean ample (J.M. Colebrook, unpublished).

percentage of the area which was free of planktonic indicators of oceanic or neritic conditions (Figure 3. A); that is, the percentage which showed evidence of mixed oceanic-coastal water. He then compared this with the strength of the contemporary haddock broods (Figure 3. B). It is apparent that the best broods were produced in years when the plankton indicated the presence of mixed water. Mr. J.M. Colebrook has provided Figure 3 (C) which shows the fluctuations in the numbers of large *Calanus finmarchicus* in the northern North Sea, from Continuous Plankton Records: the haddock brood strengths fluctuated inversely with the abundance of *Calanus*. Apart from the intrinsic biological interest of such relationships, both the planktonic measurements of the environment shown in Figure 3 (A and C) can be obtained easily and, if the relationships should prove to be valid, the plankton could be used to predict the recruitment of haddock to the fishery stocks.

A more direct application of plankton studies to fishery fluctuations has been provided by Burd (1958). It should be explained that the herrings of the southern North sea showed a striking increase in length in 1951, and this increase continued for some years. Burd, in his Figure 2, has plotted the asymptotic length of the herrings, in each year from 1935 to 1957, against the average yearly quantity of *Calanus* on the routine line of net-stations, sampled regularly by the Lowestoft Fisheries Laboratory, and known as the "Flamborough line". There is a clear relation between

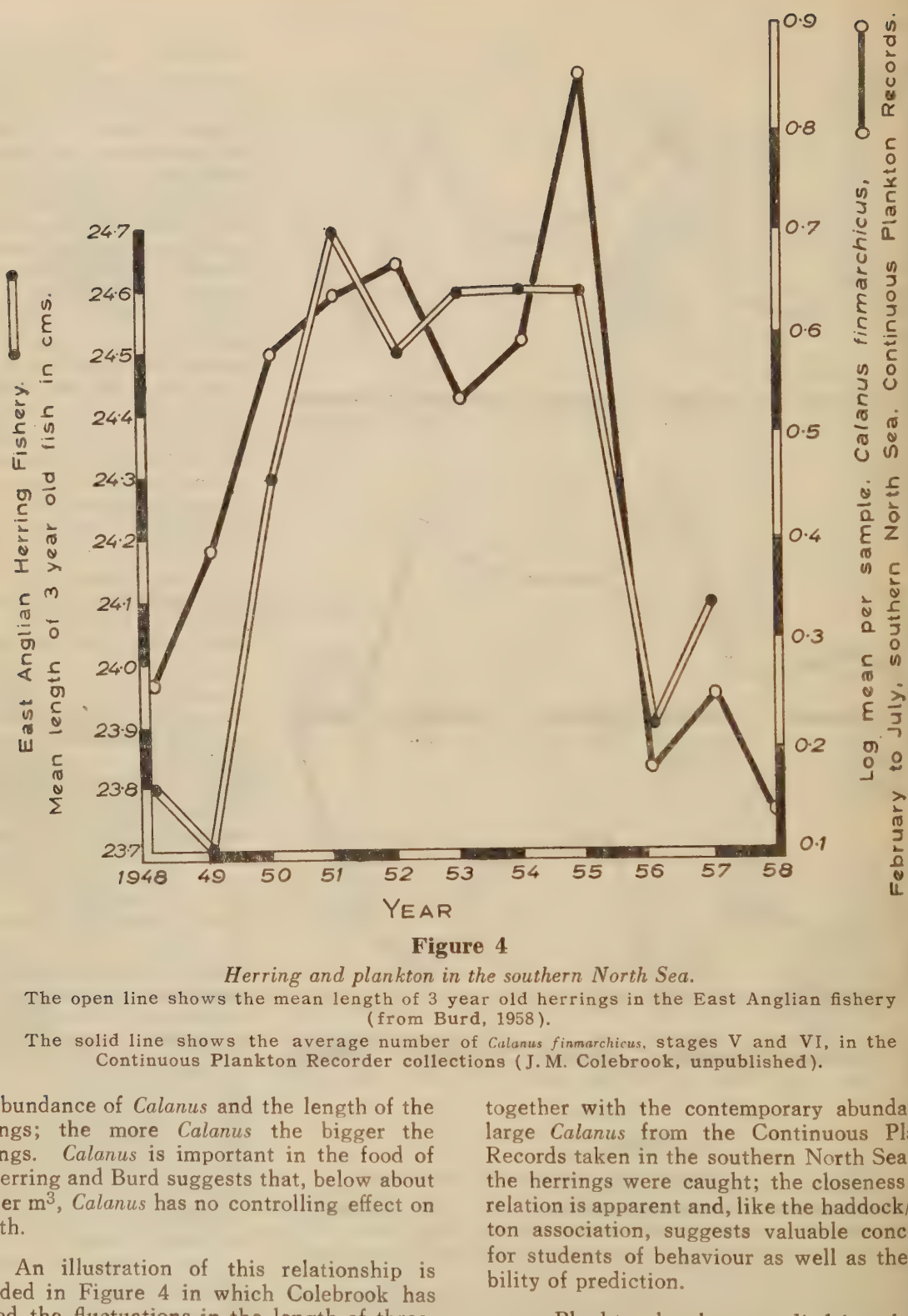

Figure 4

Herring and plankton in the southern North Sea.

The open line shows the mean length of 3 year old herrings in the East Anglian fishery (from Burd, 1958).

The solid line shows the average number of *Calanus finmarchicus*, stages V and VI, in the Continuous Plankton Recorder collections (J. M. Colebrook, unpublished).

the abundance of *Calanus* and the length of the herrings; the more *Calanus* the bigger the herrings. *Calanus* is important in the food of the herring and Burd suggests that, below about 100 per m^3, *Calanus* has no controlling effect on growth.

An illustration of this relationship is provided in Figure 4 in which Colebrook has plotted the fluctuations in the length of three-year-old herrings (taken from Burd's paper) together with the contemporary abundance large *Calanus* from the Continuous Plank Records taken in the southern North Sea wh the herrings were caught; the closeness of relation is apparent and, like the haddock/pla ton association, suggests valuable conclusi for students of behaviour as well as the po bility of prediction.

Plankton has been studied in relatio the aggregation and dispersal of herring sho

xample, Manteufel (1941), using a modified ly Plankton Indicator, and Cushing (1955), g conventional nets, have both suggested the different stages of herring shoaling viour are dependent on the gradients of dance of the planktonic food of the herring.

Routine and systematic observation of the onment of fish has been employed for some s at the Scripps Institution of Oceanography, cularly in relation to the sardine and tuna. , Roden and Wyllie (1958), in a long-term y, have suggested that the abundances of lankton and sardine are inversely related it is worth quoting from their report. Because different methods of measuring lankton were used before 1940, it is not easy mpare present populations with those in past..." Blackburn (1958) has shown a interesting positive relation between the dance of Chlorphyll A and of zooplankton ie Californian coast; and a further positive ionship between zooplankton and the nekton h constitutes the main food of the tuna ckburn's figures 3 and 4).

At the beginning of this paper I quoted extracts from the Prospectus for this Sym- um on Fish Behaviour. In a short paper it not been possible to do more than suggest field observations of the plankton are likely elp in finding an answer to the questions d by these quotations.

Knowledge of the plankton may provide the for an understanding of factors controlling physiology and behaviour of fish; it may provide the means of testing experimental theses; finally, there are grounds for believing that field observations of the plankton may provide the means for prediction of fish behaviour and fishery fluctuations.

Of all the questions which the field ecologist would like to put to the student of behaviour, probably the most important are concerned with the factors which stimulate or inhibit the aggregation of fish into shoals. The immediate success of most commercial fisheries is directly dependent on shoaling behaviour which must also play an important part in spawning, brood survival and subsequent recruitment to the fishery. But it is possible that the greatest value of field research on plankton will result from the study of the composition of planktonic communities in order to infer environmental changes which, with our present knowledge and techniques, cannot be defined and measured. Lucas' (1955) work on external metabolites has suggested the complicated nature of controlling mechanisms in the sea; the new interest in behaviour provides an excellent opportunity for field ecologists and experimentalists to work together and unravel some of these complications. In this collaboration the value of field studies of the plankton will be greatly enhanced if uniform sampling techniques are used systematically in time and space. For many areas, this may be more easily achieved if the techniques are not dependent on the availability of research ships. Apparatus must be simple and automatic in operation; planktologists must sometimes be prepared to sacrifice refinement in order to study the broad, overall picture; the immediate objective is the quantitative statement of biological fluctuations.

.3.22 Les Migrations de Poissons dans les eux Douces Tropicales Africanes

par

J. Daget *

Dans les régions tropicales du globe où nent une saison sèche et une saison humide tranchées, les crues annuelles des fleuves ent certaines espèces de poissons à effectuer déplacements saisonniers qui sont de véritables migrations, si l'on définit celles-ci: des déplacements périodiques en masse auxquels sont astreintes certaines populations au cours de leur existence. Ces migrations sont particulièrement importantes lorsque les eaux de

ef du Laboratoire d'Hydrobiologie de Diafarabé (République Soudanaise)

Indo-Pacific Fish. Coun. (III): 79-82, 1958.

crue peuvent inonder de vastes surfaces comme c'est le cas dans le bassin du Moyen Niger et dans le bassin tchadien pour ne citer que deux régions d'Afrique où la pêche constitue l'une des ressources locales essentielles. Il est évident que dans ces deux bassins situés à l'intérieur du continent africain, tous les migrateurs appartiennent à la catégorie des holobiotipues potamobies.

Il serait souhaitable de pouvoir classer ces migrations suivant la nature des mécanismes qui les déclenchent, mais nos connaissances en la matière sont encore trop imparfaites pour tenter une telle classification. Nous nous contenterons de distinguer, d'un point de vue purement descriptif, des migrations longitudinales anadromes ou catadromes et des migrations latérales. Les premières sont celles qui suivent, dans un sens ou dans l'autre, le lit du fleuve, de ses bras ou de ses affluents; les secondes sont celles qui s'effectuent dans les zones inondées latéralement par le fleuve débordant son lit, c'est à dire dans les plaines d'inondation. Migrations longitudinales et migrations satérales mènent les poissons dans des milieux écologiques tout à fait différents et doivent par conséquent avoir pour les espèces des significations biologiques distinctes.

L'existence de ces deux types de migrations est relativement facile à mettre en évidence, pour autant qu'il s'agisse d'espèces d'importance économique. Les pêcheurs en ont une connaissance empirique assez précise; en effet, toute population de poissons qui se déplace en masse est susceptible de rentrer d'elle-même dans un piège ou tout autre dispositif de capture approprié et placé au moment voulu sur son passage. Les techniques halieutiques basées sur ce principe sont nombreuses, et souvent à gros rendement. La simple surveillance de ces dispositifs de pêche et le dépouillement des statistiques correspondantes, en faisant apparaître des pointes saisonnières de capture pour certaines espèces, donnent déjà de précieux renseignements sur les lieux et dates de passage des migrations. Cependant, pour préciser les trajets suivis et l'amplitude des déplacements, il est nécessaire de faire appel à des expériences de marquage. L'utilisation des isotopes radioactifs peut se révéler précieuse pour suivre durant un laps de temps limité des poissons de petite taille ou des alevins. Mais ces techniques qui ont déjà donné dans divers domaines des résultats remarquables, resteront sans doute d'application limitée pour les problèmes qui nous intéressent ici. Les marques individuelles récupérables resteront toujours le procédé de choix. Etant donné que la croissance des poissons dans les eaux tropicales est souvent très rapide, au moins pendant une certaine saison, on devra rechercher avant tout un dispositif de marquage qui puisse rester en place et bien visible pendant plusieurs années. Au point de vue, les rondelles d'ébonite et les agrafes métalliques fixées à l'opercule ou sur les nageoires et portant un numéro de référence, donnent peut-être quelques déboires. Nous pensons que le meilleur dispositif serait une marque hydrostatique composée simplement d'un petit tube étanche de celluloïd ou de matière plastique de couleur vive, numéroté et fixé par un étrier métallique en avant de la dorsale. Le pêcheur qui capturerait un poisson marqué de cette façon s'en apercevrait immédiatement et n'aurait qu'à détacher la marque à l'intention du Service piscicole intéressé. Ce dernier devrait envoyer périodiquement un enquêteur dans les villages et les campements de pêche pour s'enquérir des reprises effectuées, collecter les marques récupérées et transcrire sur fiches tous renseignements intéressants concernant les lieux, date et conditions de capture. Un système de primes pourrait être institué afin de stimuler le zèle des pêcheurs et les intéresser au succès des expériences de marquage. Dans le Moyen Niger comme dans le bassin tchadien, la pêche est suffisamment intense pour que l'on soit assuré d'un pourcentage de reprise élevé.

Mais il convient également de chercher une explication scientifique au phénomène migratoire et de dégager les causes physiologiques qui rendent obligatoire à un moment donné le changement d'habitat. Une migration n'est qu'un aspect particulièrement aigu du conflit, condition même de la vie selon Claude Bernard, entre l'organisme vivant et son milieu; le premier parce qu'il est momentanément ou non incapable de s'adapter au second, devant chercher son salut dans la fuite. C'est donc par des diversités de condition physiologique et plus précisément de fonctionnement endocrinien, entrainant une hypersensibilité toute particulière à certains stimuli externes d'ordre physique, chimique ou météorologique, que l'on doit chercher à comprendre pourquoi, placées dans les mêmes conditions, certaines espèces ou catégories d'individus, telles qu'immatures ou adultes par exemple, entreprennent une migration alors

tres restent sédentaires. Or, dans les ons tropicales que nous avons en vue, les aux de divers chercheurs ont prouvé que les poissons ont une croissance rapide durant ériode des hautes eaux et nulle durant la ode des basses eaux. L'arrêt de croissance souvent accompagné d'un amaigrissement ible, les individus utilisant plus ou moins réserves adipeuses accumulées durant les es eaux; il est fréquent en fin de saison e de rencontrer des états de carence caracés. En outre, la reproduction a lieu à un ent de l'année bien déterminé, en général lant la montée des eaux. Nous pouvons admettre, et la preuve n'en serait probaent pas difficile à administrer, que ces sons tropicaux présentent dans le fonctionent de la thyroïde et de l'hypophyse un cycle iel à phases particulièrement bien marquées, possibilité de déséquilibres endocriniens à aines périodes critiques de l'année. Rapns que d'après les Professeurs Fage et aine, "il apparaît que fréquemment un rfonctionnement thyroïdien ou hypophysaire précéder ou accompagner le déclenchement migration." Des recherches orientées en sens pourraient aboutir à des résultats onstratifs.

Une fois les organismes physiologiquet préparés pour la migration, ce sont des uli externes qui vont déclancher le départ. exemple, on a maintes fois noté que les ations sont liées à la baisse ou à la montée eaux; parfois même on constate qu'une ode d'arrêt ou un renversement momentané le sens de variation du niveau arrête le vement. Dans tous ces cas, on peut supposer c'est la concentration tatale de l'eau en sels eraux qui a changé. Les poissons, à cause phénomènes d'osmorégulation, y sont très ibles. Or une méthode quantitative simple apide pour obtenir des donées globales sur eneur de l'eau en électrolytes consiste à surer la conductivité. On a déjà vérifié qu'il te une corrélation étroite entre les variations le facteur et certaines migrations. D'ailleurs eaux tropicales sont souvent peu minées, soumises à une évaporation importante ar conséquent les modifications locales de nductivité doivent s'y faire sentir à un taux if élevé. Dans certains cas, on a observé les mouvements migratoires étaient appaent réglés par les phases de la lune, et, du les nuits ropicalest sont pour la plupart sans nébulosité en saison sèche, c'est probablement la durée et l'intensité de l'éclairement nocturne qui jouent le rôle de stimulus. Mais le milieu externe ne se réduit pas à un ensemble de facteurs physico-chimiques, il comprend aussi, pour un individu donné, tous les êtres vivants qui l'environnent. Lorsqu'une espèce est strictement tributaire d'une nourriture déterminée, elle suivra naturellement les déplacements de cette nourriture. Ainsi les migrations de petits poissons seront suivies par les voraces qui les pourchassent. Enfin il est des migrateurs qui voyagent en bancs serrés, tous les individus se déplaçant dans le même sens, à la même vitesse et effectuant les mêmes évolutions; on peut penser qu'il existe alors un effet de groupe, c'est-à-dire que le comportement migrateur observé n'est manifesté par un individu qu'en présence d'autres individus de sa propre espèce; peut-être même y a-t-il à l'origine attraction sociale au sens où l'entendent les zoopsychologistes.

Ainsi nous voyons combien le problème des migrations de poissons d'eau douce tropicaux sont complexes et combien le chercheur devra se montrer prudent dans les interprétations qu'il en propose. Revenons sur les migrations latérales telles que nous les avons définies plus haut et envisageons seulement le cas, assez fréquent, d'espèces pondant dans le lit mineur en période de montée des eaux. Les alevins, dès résorption de leur vésicule vitelline, vont se mettre en quête de la nourriture qui leur convient c'est-à-dire de microplancton et celui-ci va se développer d'une façon véritablement explosive dans les plaines d'inondation à partir du moment où les eaux de crue s'y étaleront. Mais du fait que les alevins pénètrent eux aussi dans ces plaines, peut-on dire que leur migration latérale soit essentiellement trophique? Ne serait-ce pas confondre résultat et causes? Comment en effet les jeunes poissons seraient-ils attirés par l'abondance de la nourriture existant dans un milieu qu'ils ignorent? Il paraît plus simple d'admettre qu'au moins les très jeunes alevins sont tout simplement entrainés, en quelque sorte accidentellement par les courants souvent assez forts qui s'établissent du lit du fleuve vers les plaines d'inondation. Des individus déjà plus vigoureux peuvent faire activement et non plus passivement le même trajet, chassés du lit mineur par la concurrence vitale due à la surpopulation d'un milieu peu riche en possibilités alimentaires. En résumé, nous suggérons que les alevins pourraient très bien pénétrer dans les plaines d'inondation sans

qu'aucun facteur déterminé les y attire. Naturellement, en raison des conditions essentillement favourables qu'ils rencontrent, aucun ne chercherait à en sortir avant le retrait des eaux, d'où le fait qu'ils s'y trouvent finalement réunis en totalité. Lorsqu'il s'agit des migrations latérales d'adultes, une nouvelle interprétation surgit: les poissons n'ont-ils pas tendance, par une sorte de mémoire, à retourner sur les lieux où ils avaient trouvé l'année précédente des conditions de vie meilleures? A la décrue, lorsque le viveau baisse dans les plaines inondées, les migrations latérales reprennent en sense inverse. Le retrait des eaux oblige naturellement tous les poissons à émigrer, mais les modalités de départ sont très variables; certaines espèces ne se mettent en movement que forcées par le progrès de l'assèchement alors que d'autres à comportement migrateur caractérisé partent en masse dès le début de la décrue. C'est alors quinter'viennent les sensibilités différentielles de nature physiologique vis-à-vis des stimuli externes. Mais comment les poissons retrouvent-ils le chemin qui mène au lit mineur du fleuve, parfois très éloigné et accessible seulement par un dédale compliqué de défluents? Suivent-ils le sens d'écoulement de l'eau où sont-ils guidés par une mémoire topographique du trajet suivi à l'aller?

Pour le seul problème des migrations latérales qui aurait pu paraître assez simple a priori, nous venons de poser beaucoup d'interrogations. Or ce sont des certitudes ou du moins des éléments de réponse basés sur des faits scientifiquement controlés dont nous aurions un besoin urgent. Les techniciens étudient actuellement des progets d'aménagements hydrauliques pour irriguer les plaines inondables, régulariser les crues, endiguer les fleuves et s'assurer la maîtrise et le contrôle des eaux sauvages. Nous sommes en mesure d'assurer que de tels ouvrages auront des répercussions considérables sur les migrations de poissons et partant sur la pêc L'exemple du barrage de Markala auquel n avons consacré une récente mise au point, en une preuve permanente. Mais, lorsqu'on consulte sur les mesures à prendre pour p mettre aux poissons migrateurs de franchir obstacles dont on projette la construction, hydrobiologistes ne peuvent donner que réponses vagues et insuffisantes, faute pouvoir se référer à des données de b précises.

En guise de conclusion, nous donner les grandes lignes d'un programme de recherc pouvant être réalisé soit dans le bassin du Mo Niger sois dans le bassin tchadien qui présent l'un et l'autre des conditions topographiq favorables et pour lesquels les prospecti hydrobiologiques ont déjà été assez poussées

1) Choisir un ou plusieurs secte et une ou plusieurs espèces migratrices lesquelles on concentrara les moyen d'in tigation. Le choix sera dicté par le sc de simplifier au maximum le travail maté

2) Déterminer les aires et les é ques de ponte; préciser le cycle biologi annuel en déterminant notamment le rég alimentaire aux diverses saisons et divers âges, le rapport hépato-somati (RHS) et le rapport gonado-somati (RGS), les phases d'activité de la thyro et de l'hypophyse.

3) Etudier les variations du mili notamment les gradients de conductivité sens et l'amplitude des modifications niveau et du courant.

4) Procéder à des marquages des statistiques de pêche en des points des époques judicieusement choisies.

4. THE IMPORTANCE OF FISH BEHAVIOUR TO FISHERIES

4.0 Introduction

It is obvious that the design and use of ing gear is guided by what is known of the aviour of fish. It is also clear that fishing rations ought to be conducted so as to make of every sign signifying particular behaviour as in particular situations and significant artures from general behaviour patterns in cial situations. It is perhaps less clear that rmation on behaviour is required by those study the dynamics of fish populations, ough it is not difficult to generalise about the tions that certainly exist between certain s of behaviour and some parameters of ulation equations. However, for the pur- es of research workers of the Indo-Pacific, of the aims of this Symposium was to obtain chedule of particular instances of these ous relations and from that to formulate a to assist them to decide, with regard to ticular species and situations, the aspects of aviour on which research should be under- en. Such decisions imply that there is ionable prospect that possession of the know- ge resulting from the selected research would ble fishermen to conduct their operations h greater success, or administrators and ers to manage the resource and the fishing rations so as to improve the return from the istry.

Many items for a schedule of particular ances have been mentioned in earlier sections this report and others are given in the ions that follow.

In the prospectus of the Symposium it indicated that this aspect of the subject ld be dealt with by considering the influence behaviour on five characteristics of a fish k or population. Two of these related ctly to strategy and tactics of fishing, the r three to population dynamics. The mani- ations of the latter (population dynamics) the magnitude and composition of the stocks fluctuations in these; with regard to these ifestations people in industry and govern- t must make decisions on the nature, pattern intensity of fishing, leading to management of industry. Hence we may group the questions ed in the prospectus in the following way:

Implications for fish searching and fishing techniques:

Distribution
Liability to capture

Implications for management:

Reproduction
Growth
Natural Mortality

These, however, are very general; it will be well to transform them into practical questions formulated from the experience of fishermen and research workers; we may give some examples of these questions within the foregoing framework. However, there is a general observation to make before setting out these questions. Although every behaviour pattern or set of actions has a more or less fixed form, it, as indicated in Section I, is displayed in relation to various elements of the environment and is subject to interaction between organism and environment. Some of the environmental elements exercise indirect influence on behaviour by determining the well-being of the organism and its capacity to perform actions; other elements act as stimuli of various kinds, as discussed in Section 2. None of these elements is completely stable, with respect to time or space, and in consequence each behaviour pattern is liable to some variation as to place and time at which it is manifested. One of the tasks of the fishermen and research workers is to discover signs that will indicate with precision where and when a particular event will occur. Beyond these normal variations the behaviour patterns are subject to major disturbances that may lead to very important departures from normal occurrence (*e.g.* appearance of a species in an area in which it is rarely seen) and to states of stress or displacement. In some cases, at present notably in inland fisheries, preventive or remedial action against such harmful environmental changes may be possible.

In reading the following schedule it is to be understood that each question implies a search for an assessment of a normal pattern

with its range of circumstances and manifestantions, and something of the possibility of extreme variations. Each question also implies that the answer will show how occurrences may be detected and how, in some cases, fishermen might benefit by modifying their equipment and methods, in other cases what might be done by management (industrial and governmental) (a) to secure best deployment of fishing power, (b) to prevent, offset or remedy calamitous effects, or (c) to improve or develop resources.

Implications for fish searching and fishing techniques:

Distribution

1) where will the fish be at a particular time or, conversely,
2) when will the fish appear at a particular place?

Liability to capture

3) what is the aggregation aspect of the fish on the fishing grounds: Schooled or dispersed?
4) are the fish temporarily halted on the grounds, or moving through them?
5) what is the activity of the fish on the grounds: feeding, nesting, spawning, etc.?
6) what is the reaction of the fish to various natural forces when on the grounds?
7) What is the reaction of the fish on the grounds to various artificial stimuli: chemical, electrical, mechanical, light, visual forms, etc.?

Implications for management:

Reproduction

8) what effect on spawning mi tion is produced by var environmental changes, inc ing those made by man?
9) what effects on spawning haviour (site selection, n building, fertilisation, care young, etc.) are produced environmental changes?

Growth

10) what factors (or values of tors) can interfere with finding of feeding grounds, with feeding?
11) what abnormal values of envi mental factors can lead behaviour of a kind that interfere with growth?

Natural Mortality

12) what abnormal values of vironmental factors can lea behaviour of a kind that cause the fish to be more sus tible to lethal values of phys and chemical factors, preda and disease?

More precisely practical formulation questions such as these will be found in papers of this section, with some indication how the answers are being sought and of s of the answers obtained.

4.1 Implications for Fish Searching and Fishing Techniques

4.11 Preliminary Results of Underwater Observations of Tuna Schools and Practical Applications of these Results

Donald W. Strasburg and Heeny S.H. Yuen *

0. INTRODUCTION

Recent findings of the Pacific Oceanic Fishery Investigations (POFI) suggest that the oceanic skipjack, *Katsuwonus pelamis*, repres the largest tuna resource in the central Pac Ocean. Studies of larvae, capture of adults several methods, and sightings of surf

* Fishery Research Biologists, Pacific Ocean Fishery Investigations, United States Fish and Wild Service, Honolulu, Hawaii

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ols all indicate that this species is not only ly distributed but also frequently abundant opical and subtropical Pacific waters.

In spite of their distribution and numbers, jack are not harvested to the degree anted by the world's increasing demand for ein. Probably the principal reason for this e fact that the fishery is prosecuted by live- methods, for which the bait is usually ate (precluding long voyages to the fishing nds) and in short supply. Several approaches ne problem of increasing skipjack landings therefore centered on the fishing method: to develop gear to catch skipjack without (2) to use presently unexploited bait ies, and (3) to increase the efficiency of the ent methods.

In the first approach are gill-netting and e-seining, both of which have been tried by I, and neither of which has proved satis- ory in tropical waters of the central Pacific. er baitless methods of capturing skipjack are being studied. POFI has also been in- sted in utilising new bait species and easing the supply of the present kinds. The lts of these studies are promising but far complete. In the third approach which is subject of this report, POFI has studied the ibility of increasing efficiency by modifica- s in techniques that might be suggested by er understanding skipjack behaviour as ed to several fishing variables.

. DESCRIPTION OF THE FISHERY

Before discussing skipjack behaviour it ld be well to describe the skipjack fishery as now conducted in the Hawaiian Islands. Hawaiian fleet consists of 26-30 vessels, lly known as sampans or aku boats ("aku" e Hawaiian name for skipjack). These ships rom 60 to 80 ft. long and weigh 27-77 tons. ir crews number 7-15 men, all but two of m fish. The deck house is located well ard, leaving a clear working space of -600 square feet aft. In this space are ated wells for carrying live bait and iced age spaces for keeping the catch. Around stern is a series of pipes fitted with nozzles; n fishing is in progress sea water is pumped ugh these pipes to produce a spray that es the sea and supposedly enhances the ts of the bait employed.

After obtaining a sufficient quantity of live bait, usually nehu (*Stolephorus purpureus*, a small anchovy), from inshore waters, the sampans depart for the fishing grounds, getting under way before dawn so as to make maximum use of daylight while on the grounds. A considerable part of their day is devoted to scouting for tuna, by searching for flocks of sea birds with the aid of binoculars. These birds feed on the small fish and squid driven to the surface by skipjack, and their presence is thus indicative of tuna. When a feeding bird-flock is sighted it is approached and when the boat is judged to be close enough, one of the fishermen throws live bait into the water as chum, and if this is successful the skipjack school converges on the bait. The water sprays are then turned on so that droplets strike the sea in a large arc around the rear of the vessel, and the fishermen take their places at the stern.

Fishing is done with bamboo poles equipped with jigs of various sorts, the hooks of which are barbless and nearly always unbaited. Jigs are cast into the water where the sprays strike, and the combination of the activity of the live-bait, the spray splashing, and the fall of the jigs resembles the effects produced by a school of small fish. A hooked skipjack is pulled from the water and caught under one arm by the fisherman, who slides the hook from its mouth, throws the fish on the deck behind him, and returns his jig into the water. Fishing usually lasts 15-20 minutes; when it ends the fish are iced, the deck cleaned, and another school sought. Because of bait mortality and the fact that the catch is iced rather than frozen, fishing is done within 100 miles of shore, and typical trips are of only one day's duration. The catch per trip may amount to as much as 40,000 lbs. of 3-35 lb. fish. During the summer skipjack season most of the catch is composed of 18-22 lb. fish.

2. UNDERWATER OBSERVATIONS

POFI's initial work on tuna behaviour has been an attempt to assay several of the variables apparent in fishing conducted as above. Among the items investigated were the effects of: water sprays, chumming rate, live versus dead bait, noise, various bait species, and seepage into the fishing area of certain body fluids from fish lying on deck.

These variables were studied both from the surface and from an underwater observation chamber attached to the side of the POFI research vessel *Charles H. Gilbert*. The observation chamber is a 14 ft. steel cylinder equipped with windows at its lower end, and mounted so that it can be lowered until the windows are 6 ft. beneath the sea surface. Coloured movies were taken of underwater tuna activity, and were supplemented by recorded spoken comments from underwater and surface observers. Catch rate was noted by ringing a bell each time a fish was hooked, the bell tones also being recorded. In addition, samples of the fish caught were measured and their sex organs and stomach contents examined.

The following routine was used in conducting sea experiments on skipjack. Baiting and scouting were done as in the commercial fleet, with the exception that this work would be done only in sunny weather and relatively calm seas. The former prerequisite ensured sufficient light for underwater photography, the latter reduced turbulence and splashing into the open top of the observation chamber. Part of the illumination problem was solved by selecting a relatively fast colour film with which pictures would always be taken between about 9 a.m. and 4 p.m. unless the sky was heavily overcast.

When a skipjack school was encountered it was approached closely and chumming begun. If tuna responded to the chum, the chamber was lowered rapidly (1½ minutes) and the vessel's speed decreased to reduce turbulence and allow fishing to commence. In most cases the initial fishing was done in commercial manner and the exposed to record skipjack behaviour under film these conditions. In nearly all experiments periods of "commercial" fishing alternated with experimental fishing, this being necessary in order to detect changes in behaviour with time, i.e., skipjack activity could change as the appetite for bait became satiated.

Before discussing the experimental results it would be well to mention the general appearance and behaviour of a typical school of feeding skipjack. In Hawaiian offshore waters an underwater observer's field of vision extends to about 60 ft. for skipjack. Tuna of more than 5 lbs. weight are identifiable to species within this range, although it is difficult to see their distinctive colour patterns in the outer parts of this field. Probably of greatest interest in live skipjack identification is the optical suppress of the blackish belly stripes and the promine given to a series of dark spots resembling p marks along the midsides. These spots disapp immediately after a skipjack is landed, at wh time the familiar dark belly stripes become m more noticeable than they ever are when s underwater.

The activity of skipjack varies marke with size. The smallest skipjack seen w about 20 cm. in length, and thousands of th fish schooled together. Such schools w noteworthy for their seemingly instantane response to stimuli, precision in manoeuveri and the close spacing of individuals. In c parison to larger fish, it seemed that schoo was a dominant trait in the behaviour of th small fish, for the schools never entirely disru even during feeding.

In medium-sized skipjack (45 - 65 cm. 4 - 14 lbs) activity was frenzied and m semblances of schooling were lost during feedi The fish made rapid dashes to the surface, eit singly or in pods of half a dozen fish, at spe difficult to measure but probably close to knots. Such fish pursued chum at veloci sufficient to carry them out of visual ra Their swimming was seldom horizontal instead oscillated vertically in a pattern res bling a series of sine curves.

Large skipjack (70 - 80 cm., or 18 - 28 l appeared to be almost lethargic in compari with the smaller individuals. There were signs of schooling during feeding, and the never appeared to swim faster than about knots (more often they cruised along at 2 knots). Their swimming was horizontal nearly so, and surface dashes were relativ unhurried.

3. EXPERIMENTS

The following comments on skipj behaviour were derived from only three mont work, a large part of which was devoted developing observational techniques and sear ing for tuna upon which to experiment. Beca the data are few and only incompletely analys it must be emphasised that the conclusions tentative.

One of the first fishing variables exami was the effect of water sprays on skipj behaviour. Four skipjack schools were fis

e the sprays were turned on and off at rvals. Differences between the sprays-on sprays-off conditions were not striking, the ral picture being that the fish remained the surface (1-3 ft. depth) with the sprays ut deeper (6-20 ft.) with them off. There e more dashes to the surface when the sprays e on, and the catch rate was also higher at time. All of these phenomena are tendencies er than distinctly overt responses, for they e seldom all observed at the same time. It ld seem that water sprays cause more tuna e caught by increasing their feeding frenzy, er by making it seem that the baitfish are e numerous and by enhancing their appance, or in some other manner.

The second fishing variable studied was response to live and dead chum. As tioned earlier, the baitfish normally used was . Schools of skipjack were twice brought e stern with live nehu, and then chumming alternated between live and dead nehu. ause of their delicate nature some nehu were l or dying during the "live" bait parts of tests, and skipjack were observed to eat ary dead individuals under both experital conditions. It could not be determined ther skipjack actually ate quantities of dead in the "dead" bait sequences, but occally they swam through dense masses of dead seemingly without consuming any of them. artial explanation of our failure to detect ing here is the fact that as more and more l nehu entered the water the swimming d of the tuna decreased, dashes to the ace became infrequent, and the skipjack fell rn of the vessel where they were not clearly le to us. Had their falling behind been wed to continue, the tuna school would have n lost. Switching to live bait at this juncture lted in the skipjack returning to the fishing , increasing their swimming speed, and ing numerous dashes to the surface.

Experiments have been designed to be e in the future to determine whether mixs of live and dead nehu constitute acceptable n for skipjack. If they should prove to be the fishermen could effect a considerable saving, which would be a great advantage e bait mortality is now a serious problem. to be investigated is the problem of whether jack eat dead chum without prior or coning stimulation by live chum. Knowing something about this is vital in evaluating the stimuli released by bait, and could lead to the selection of better bait species and lures, or to the more efficient use of present kinds.

Another fishing condition examined was the rate of throwing chum. Although this varies with the type of school and the phase of fishing, there exists a normal rate which preliminary calculations show to be about 1½ lbs. of bait per minute. For the experiments undertaken, the normal rate was considered as standard, twice the normal rate as fast, and half the normal rate as slow. The chumming rate was varied during the course of fishing three skipjack schools, each of which was first brought near the vessel with chum thrown in the usual amounts.

When small schools were subjected to fast chumming, more nehu than the skipjack could consume soon accumulated. The swimming speed of the tuna increased as they pursued the abundant food, but because the nehu tended to drop astern of the vessel, the feeding tuna were also left behind, resulting in decreased catch. This was not true for large schools in which the fish were sufficiently numerous to cope with the chum immediately. In such cases activity was not increased and the behaviour of the fish appeared to be the same as that when the chumming rate was normal.

With slow chumming the skipjack swam at lower speed and tended to scatter; vertical movement, which appears to be a part of the feeding frenzy, ceased, and the tuna remained close to the surface. Clearly slow chumming provided too little food to elicit a desirable feeding response, in contrast to rapid chumming which made the bait more attractive than the jigs. Switching to normal chumming rate resulted in a return to a desirable degree of activity.

Another variable subjected to test was the effect of vessel noise on skipjack. Sound was produced by hammering on the ship's metal hull from within the engine room, but no differences in behaviour were detectable between the noise and no-noise conditions in the single school tested.

Two other bait species were compared to nehu with respect to their effects on skipjack behaviour. For these tests skipjack were first brought to the stern with nehu, and then chumming was alternated between nehu and the species under test.

Tilapia mossambica 1½-2 inches in length were tried on one skipjack school. Skipjack were not observed to feed on tilapia, their speed and frequency of dashing to the surface slackened, and they tended to group together in a partial school formation. The catch rate dropped off at the same time. Chumming was twice switched back to nehu upon which the tuna lost all semblances of schooling and their activity increased markedly. Tilapia were available for behavioural testing only on this single occasion, the results of which are at variance with numerous other trials where skipjack responded as favourably to tilapia as to nehu. Differences between the behaviour of tilapia and nehu are the subject of future studies in which it is hoped to learn more of the qualities of a desirable bait.

Approximately 150 *Dorosoma petenensis* (threadfin shad) were chummed alternately with nehu while a school of skipjack was being fished. These shad were silvery in colour, about 3-4 inches long (twice the size of nehu), and rather deep bodied, so that they were quite conspicuous as compared to nehu. Presumably their greater size and conspicuity caused the shad to be more readily taken than nehu, and these factors also caused their predators (skipjack) to strike them from greater distances and at higher velocities. The momentum of skipjack eating shad carried them away from the fishing area. Moreover shad that escaped immediate consumption took up a position 15-20 ft. from the vessel whereas nehu took up a position 2-10 ft. from the vessel, and this relative remoteness of shad as bait caused relative dispersal of the tuna preying on them. When shad were used as chum the catch rate declined, not only for the above reasons, but probably also because the lures in use were designed to compete with nehu, not with the more conspicuous shad.

Although threadfin shad and nehu had about the same swimming speeds, the use of the former caused a general dispersal of the skipjack. There is little doubt that shad are desirable bait, particularly if their high conspicuity causes the tuna to draw in from greater distances. It would be desirable for shad to remain closer to the fishing vessel, however, and perhaps this can be achieved by subjecting them to tranquilizing drugs prior to use as chum, an experiment planned for the future.

Two other effects of fishing were examined, both dealing with variations in skipj behaviour caused by draining of fish body flu from the deck of the fishing vessel. Fisher believe that blood from the catch draining the fishing area causes skipjack to bec frightened and to cease biting. In commer fishing therefore, all scuppers and other op ings in the deck are plugged during skipj fishing, and every effort is made to confine bl from the catch to the deck. To test this gallons of blood were obtained from liv skipjack and mixed with an equal volume glycerol-citrate anticoagulant. The resultan gallons of preserved blood were sprayed into sea at intervals during fishing. The blood mu with sea water quite well, forming a transpa cloud of a light red colour, through wh skipjack moved at random, showing no si of fright or other abnormal behaviour. As fish progressed numerous skipjack accumulated deck, and blood from them was allowed to dr into the sea through the scuppers. Here skipjack were observed to enter the stained wa freely with no apparent changes in behavi Later the ventral aorta was severed in half a do skipjack, and these still-living fish were tos into the fishing area. The bleeding tuna soun vertically upon striking the water, but in case did they or their blood produce any respo from other skipjack.

A second test was devised to determ whether the expected behaviour changes w caused by the colour of the blood or its chem properties. Inert red food colouring was spra into the sea in the same manner as blood been, but because it was highly concentra this dye formed a deep red-purple cloud wh was opaque in many places. Without except the skipjack avoided this deeply stained bl of water, swimming around or beneath it never through it. Five to ten minutes later ship entered the dyed area again, the col having diffused considerably in the meanti Although the sea water was still purplish colour it was transparent, and skipjack igno the dye so far as could be determined.

The results of these tests are interest in that the blood experiment tentatively proves a rather firmly entrenched belief, w that with dye suggests that skipjack co perhaps be guided or even corralled by a s ficiently dense wall of colour. Experime

ıg lampblack to create a very dark wall of our are now being undertaken, with the idea if a skipjack school can be contained within a wall, then perhaps dyes will become uable adjuncts to purse-seining or gill-net-. Academically the lampblack tests are of rest for the information they may yield about utility of "smoke screens", such as the y clouds produced by squid, against natural dators.

In addition to blood, a certain amount of slime drains from the catch during fishing, it was thought that this might contain the ine—or pterine—like substances noted by Frisch (1942) as causing a fright reaction fish. To see whether this occurred, crude acts were prepared from fresh skipjack skins removing all flesh, cutting the skin into es, and then reducing it to a semi-fluid by ns of an electric blender. One lot of the ltant liquid was filtered to give a pale straw ured, transparent fluid, the other was left in natural grey, opaque state. Both solutions e sprayed into the sea during fishing, but no nges in skipjack behaviour were seen, and ainly no fright reactions were produced. It ld be noted, however, that it was uncertain ether the extracts actually contained the nes or pterines in question.

4. CONCLUSIONS

Summarising the results of the above eriments, it is apparent that successful skipjack fishing depends upon disrupting the schooling tendency by creating and maintaining a feeding frenzy. This activity seems to be released initially by the movements of small silvery prey, and it is enhanced by spray droplets striking the water. If the feeding stimulus is made too intense by using too attractive or too abundant bait, the fishing jigs are ignored, and if it is too small, such as when unattractive or insufficient bait is used, skipjack either scatter or re-form into schools. Neither sound, blood or skin extracts appear to have much effect on actively feeding skipjack.

These conclusions are derived only from a small body of data, but in spite of this disability it is apparent that behaviour studies may be of aid to the fishery. As more is learned about bait-skipjack interactions, it becomes easier to select desirable bait species, and experiments such as the dye tests may lead to the development of entirely new fishing methods. The accumulation of more or less academic information on the structure of skipjack schools may also be of value in explaining certain vagaries of fishing: what portion of a school actually feeds at one time, whether skipjack or bait will approach a hull of one colour more closely than another, etc. Thus we feel that skipjack behaviour studies have direct practical application to problems of the fishery, as well as being of considerable academic interest.

4.12 Fish Behaviour with Special Reference to Pelagic Shoaling Species: Lajang (*Decapterus* spp.)

Soemarto *

0. INTRODUCTION

Fishery research in Indonesian waters is in the initial stage, and preference is given esearch of species of economic importance, n as the Kembung (*Rastrelliger* spp.), the ang (*Decapterus* spp.), the Lemuru (*Sardi-* spp.). Of these, the Lajang (*Decapterus*) is widely spread in the Indonesian waters is of important significance, primarily to fisheries in the Java Sea.

Most previous research on these species was directed to increasing the efficiency of the lures which are used in an important fishery whose catch is largely made up of Lajang.

In Indonesian waters, the Lajang is known as a seasonal fish appearing at definite times. In the Java Sea it has considerable significance and if the fish season comes, several home industries like "pindang" manufacture (cooking fish with salt in earthen pots) will

ssistant Biologist, Sea Fisheries Service, Djakarta, Indonesia

. *Indo-Pacific Fish. Coun.*, (III): 89 - 93, 1958.

come to life. Generally, fishermen do not pay much attention to the kind of species caught, for what is important to them is the quantity of the yield. This makes a difficulty for an official in charge of making observations on Lajang fish, who quite often finds to his dismay that these boats have no Lajang fish, but instead have other species such as Sardine, Salar (*Caranx* spp.), Mackerel, Bawal *(Stromateus)*, etc., also caught in great quantities at the time the Lajang occurs in abundance. Situations like this are felt in the fishmarket place in Djakarta (Pasar Ikan), from which the fishing grounds of the Lanjang are located farther than those of other species which are also much found during the same season.

Because the Lajang is stenohaline, salinity is an important element in its investigation. In his theory on the movement of the Lajang in the Java Sea, J.D.F. Hardenberg has given priority to the condition of the monsoon.

1. TAXONOMY AND DISTRIBUTION

The term "Lajang fish" is applied to species of the genus *Decapterus*, *Decapterus russelli* and *Decapterus lajang* species are commonly found in the Java Sea. The species *Decapterus kurroides* which is known by the local fishermen as "Malalugis" or "Momar", is found only in the waters of Maluku (Moluccas), Menado and Sangir (North Sulawesi/Celebes). In the Java Sea the Lajang is caught at approximately 20 miles from the shore.

2. OCCURRENCE OF THE LAJANG IN THE JAVA SEA

Although the Lajang can be expected to appear each year in the Java Sea, the exact time of this appearance cannot yet be predicted. Fishermen along the coast of Tjikampek (West Java) have a primitive way of forecasting the coming Lajang season by looking at the young leaves of the rhizophora trees which are numerous in that area. This method has a basis in fact, for the young leaves of the rhizophora begin to appear at the beginning of the rainy season, and in J.D.F. Hardenberg's theory on the migration of the Lajang in the Java Sea there is a similar association between the Lajang and the moonson.

If an examination is made of producti at Lajang fishing places, it is obvious that tw a year there is overproduction. Maximum yie are obtained between January and Februa March and between July and August/Septemb at the time the rainy and the dry seasons rea climax. It seems that the Lajang dissappe during the turn of the monsoon, as a result which production decreases enormously a sometimes fails completely.

The appearance of the Lajang in defin places each year cannot be exactly determin The season can be sometimes earlier or la It happens in some seasons that production Lajang is disappointing at a particular local and even that there may be no production at Such effects are produced by the monsoon wh causes the movement of the water in the J Sea. In order to analyse the migration of Lajang which follows and adjusts itself to high salinity of the water, a scheme indicati the movement of the water in the Java Sea given. This fact will be evident if the situat of the water salinity at places where Lajang caught, could be adjusted.

During the rainy season the wind blo from the west and as a result the drift mo eastward. On the contrary, during the season the direction of movement of wind a drift is reversed.

The Java Sea is much influenced many rivers flowing into it from the islands which it is enclosed. Besides the freshwa flowing from these rivers, clear, high salin oceanic water flowing from the Indian and Pacific Oceans has an influence in this sea. T alteration of direction of drift interacts w these two influences to produce a salinity cy the Java Sea water which can be summarised follows:

During the dry season, when the w blows from east to west, clear water with h salinity flows westward from the Flores Sea i the Java Sea. Simultaneously, oceanic wa from the Pacific flows southward through Strait of Makassar and, under the drive of wind, moves westward into the Java Sea. cordingly, during the dry season the Java is filled with water of oceanic nature from areas.

The Lajang fish, whose area of distribu- is supposed to have its centre in the vicinity he island of Bawean in the Java Sea, move stward with the drift, following the water h high salinity, and in this way its migration is more widely extended. However, it is correct to say that the Lajang *migrates* west- d during the dry season, it would be more t to call this westward movement a dispersal ne west.

The mature fish spawn in the environs of rean island. It stands to reason that the s and larvae which are still of planktonic are will move more quickly with the drift the mature fish, and this is why small ng fish are caught at places west of the d of Bawean (Pekalongan, Tegal, Tjirebon) re the big ones appear there.

This westward dispersal has no apparent ial purpose, for the Lajang enters waters of able salinity simply for survival and by doing t reaches the neighbourhood of the Thou- ls Islands, north of Djakarta. During the of the monsoon, the fishermen of these ds do not catch Lajang as they did during previous months.

Hence, approximately during the months ne or July, fishermen begin to catch small ng fish. If the east wind blows incessantly, fish that are caught several weeks after that igger, and total production increases.

When the turn of the monsoon comes n, production decreases and at last the fish ppears totally.

During the wet season the wind blows the west and consequently the direction of drift in the Java Sea changes. The water h flows westward during the dry season es to the east in the rainy season. From the h-west direction, water from the South ese Sea flows through the Straits of Gaspar Karimata into the Japan Sea. This water so of oceanic nature, like the water flowing the Flores Sea, namely it is clear and of salinity. Simultaneously, water of oceanic re from the Indian Ocean enters the Java through Sunda Strait. Just like the water h flows from the east, this water divides two directions, namely to the north, and to outh drifting along the north west coast of sland of Java. Many Lajang fish are caught in these waters during the months of January and February, as are other stenohaline fish from the Indian Ocean, e.g. the Tongkol (*Euthynnus* sp.) and the Tengiri (*Scomberomorus* sp.). At that time, species found in the area south of the Thousand Islands, are also caught north of the islands.

From the above information, the Lajang fish occurring in the Java Sea can be distinguished according to its origin, as follows:

1. East Lajang, which originates from the east and enters the Java Sea during the dry season by following the western drift.

2. West Lajang, which originates from the west and enters the Java Sea by following the water from the Indian Ocean.

In the western part of the Java Sea the catch normally consists of both West Lajang and East Lajang; if in any season one of these two groups does not appear, then it is obvious that the production of Lajang will be lower than normal. If for instance, the wind does not blow strongly enough during the rainy season, it is quite possible that the West Lajang will not appear, and the same may happen with the East Lajang.

There is a possibility that these two groups of Lajang fish have their own migration/dispersal boundaries, or that both groups mix in a certain area at definite times during the year.

There is a possibility that there is still another group of fish that comes from the north (South China Sea), and which could be called the North Lajang for simplicity, entering the Java Sea through the Gaspar and Karimata Strait during the rainy season. However it is still unproven that such a group does have separate existence.

In the beginning it was doubted whether the Lajang from the South China Sea could pass through Karimata Strait, because it was thought that pollution of this water and the magnitude of fresh water inflow from rivers in Kalimantan (Borneo) would be an obstacle to Lajang movement.

From investigations which were particularly directed towards the salinity of the water

and the plankton situation in the Gaspar and Karimata Straits (M.S. Zuiderkruis, May 1937), it is evident however that these two straits do not form an obstacle for the migration of the Lajang from the South China Sea to the Java Sea and vice versa. Accordingly, the presumption of the existence of the North Lajang is acceptable.

Another opinion supporting the presence of the North Lajang in the northern part of the Java Sea is based upon the following facts. There is a section of the western side of the Java Sea, triangular in shape, where the water has a lower salinity compared with the other areas of the Java Sea. The western boundary of this area is formed by the east coast of South Sumatra and the coast of the island of Bangka, which form the base of the triangle; the points of this triangle, however, are not constant in position to time but move from time depending upon the season; the apex of this triangle lies in the vicinity of "Etnadroogte" and during the rainy season lies more eastward. The Lajang is not found within this triangle because of the low salinity of the water.

During the rainy season the West Lajang is caught at places south of the triangular area, and Lajang is also found several miles north of Etnadroogte. The latter cannot be West Lajang, because northward movement of the West Lajang will be prevented by the triangular area with its low salinity. It also cannot be the East Lajang, because the drift in the Java Sea, which at that time is eastwards, would be too strong for the East Lajang. There remains only the one possibility, namely that this must be the Lajang originating from the South China Sea moving southwards following the water through the Gaspar and Karimata Straits.

The triangular area with its low salinity prevents this North Lajang from dispersing farther South, and accordingly it will not be found in the vicinity of the Thousand Islands or in the Bay of Djakarta.

From the above information, the following conclusions can be drawn. The East Lajang group which is found in the vicinity of the island of Bawean can be met in the Java Sea throughout the year. During the dry season this group of fish disperses westward, following the drift, and during the rainy season it is driven back to the east at the time that the west Lajang, from the Indian Ocean, enters the Java Sea through t Strait of Sunda. In addition North Laja disperses from the South China Sea during t rainy season.

It is desirable now to study further t movements of these three groups, to determi the limits of distribution of each and to measu the intensity and locality of mixing. Taggi methods will certainly be important in su work.

3. BEHAVIOUR OF FISHES NEAR THE LURES

The efficiency of fish lures has be studied by several fisheries experts; the ch problem being to ascertain what it is that lea the fish to seek the environment of the lu J. Reuter (1938) who studied the movement fishes around lures could not decide whet the fish were in search of food on the cocoan leaves, which are covered, with algae, or w simply seeking shelter.

J. Keus has concluded that the fish lure used as hiding-place by the fish. The conclusi is based upon several facts, among others presence of fish which is always found in sho around the fish lure in an upstream position. is noticeable that small fishes like to shel under floating things, and in the neighbourho of sunken objects to avoid the attack of predato Pelagic plankton eaters such as the Lajang, l in shoals, which is itself a means of defence, shoal forming a shelter for each individual. T fish rarely behave calmly within the shoal, a on meeting the smallest danger, the shoal w turn and move to a quiet place.

Generally, fish lures are anchored places with clear and flowing water, under wh conditions they prove to be more attractive fish. Usually, such places lie offshore ab 30 - 60 miles.

The species usually attracted by lures a in addition to Lajang (*Decapterus* sp.), Kembu or Mackerel (*Rastrelliger kanagurta*), Se (*Caranx leptolepis*, *Caranx mate* etc.), Temba (*Clupea fimbriata* etc.), and Bawal (*Stromat* sp.). These species are usually caught toget with Lajang. These fishes are of species provided with protecting organs on their bo

se organs are usually to be found within the nd" zone. The size of this "blind" zone es from species to species. That of the al *(Stromateus* sp.*)* for instance is bigger i that of other fishes; and although the body ompressed, its movements are like those of with a round body. Fish of this species ays swim as though aware of danger. This ecause if this fish swam with its body held ically, its visual area would be very limited pared with fishes with a round body. This erhaps the reason the Bawal *(Stromateus* sp.*)* ays looks for a fish lure in which to hide or ter.

Fishes found upstream from the lure often e, but are always found at the same depth get their food in this area. The fish are ected in the rear by the lure, which will per any enemy that might come within the e of their "blind" zone. In searching for l the shoal of fish does not remain constantly ne place, but moves to the right and to the and always returns to its original position. here should be danger from behind, for ance from attack by a predator, the lure ntens the attacker and causes it to withdraw consequently to come into the visual range the small fish which quickly move and roach the lure for shelter.

It once happened, that a shark approached oal of fish near the lure. The shoal of fish ained quiet and the shark which was below shoal moved upwards step by step to attack ut at the same time the shoal also made the e movement and gradually nearly reached surface of the water.

The extent of the shoal of fish which ter around the lure varies. During the ng season for instance, quite often shoals of ng are found which are not near fish lures frequently noticed near the island of Bawean e Java Sea.

The fact that lures anchored at places clear water are more attractive for the fish be proved by making comparisons of the ls from various places. In the eastern part he Java Sea, where lures are anchored at es with clear water, the catch per haul is noticeably more than that in the western part where the water is dirty.

According to Keus, the presumption that the fish feed on the rotting cocoanut leaves is incorrect, for if it were true, the fish would be found downstream of the lure, while in reality the reverse situation is true.

Generally, fishing operations near the fish lures are carried out in the morning from daybreak (sunrise) up to nine o'clock or in the afternoon towards twilight. During these times the fishes are found near the surface, because of the presence of the plankton at that time and this feature is efficiently used by the fishermen. Besides fish lures, fishermen use light to attract the fish, e.g. the light of a kerosene lamp of 300-400 candle power. Several kinds of fish attracted by light will gather around the lamp and at first behave very excitedly, but after a while they become accustomed to the light and swim in disorder in a great circle.

A poor catch, taken with a payang net in the Strait of Bali in 1953, had the following composition : of the 280 fish of the total catch, 80 were Lajang *(Decapterus* sp.*)*, and the other 200 were Clupeids, of which the greatest part *Sardinella allecia* (Raf), with a few *Clupea leiogaster* C.V. and *Clupea fimbriata* C.V. Further examination indicated that the stomachs were half filled or empty. Copepoda *(Calanus* sp.*)* which was mostly in perfect condition was found among the waste in the stomach.

Further research concerning the stomach contents of the Lajang *(Decapterus* sp.*)* has been carried out in the neighbourhood of the island of Bawean (Java Sea) and it can be concluded that the Lajang is in search of food at definite times of the day. Lajang caught in the morning have empty stomach, except for hard food-remnants that are difficult to digest. On the contrary, fish caught in the evening have full stomachs, containing half-or undigested food. On the contrary, fish caught in the waters of Djakarta, always have some food in the stomach whether caught in morning or afternoon. Of the stomach contents of the Lajang, the zoöplankton include identifiable Crustacea, Copepoda, Chaetognatha, Gastropoda and fish larvae.

4.13 On the Behaviour of Lemuru, Sardinella Allecia (RAF.) at Bali Strait

R. Soerjodinoto *

1. MATERIAL STUDIED

The sardine like fishes found in Bali Strait, are of several species of which *Sardinella allecia* (Raf.) is the most abundant. Bleeker first named this species *Clupea (Sardinella) lemuru*; afterwards Weber and de Beaufort named it *Clupea (Harengula) longiceps*. This species is found in several waters, as e.g. the South China Sea, the Atlantic, Mediterranean and Black Sea.

In Indonesia this species is concentrated mainly in Bali Strait. During the "lemuru" season, which is usually wet, species other than this are caught. At the beginning of the season squid is caught in great quantities but this gradually disappears and as it does the sardine-like fishes occur in great abundance.

At the end of the "lemuru" season, the "lajang" or horse mackerel is found in great quantities.

2. THE FISHERIES

The fishery for these sardine like fishes, which is carried out by the local population of Muntjar, has not yet reached an intensive stage. There is still much to be improved. Since many of the fishermen of Muntjar come from different places, the gears they use are heterogeneous. They usually come from Panarukan, Besuki, Kalibuntu (all situated at the coastal area of the Madura Strait), Kraksaan (East Java) and even from the isle of Madura. The gear in most common use is an encircling net provided with a bag. The local name of this gear in Panarukan is "pajang".

The fishermen of Muntjar, however, used the "djala ura" (seine), while the fishermen from Tratas (South of Muntjar) use the "djala rompo" (seine). The difference between these gears lies only in the measurements for in principal they are all the same. The "pajang" is generally ± 160 m long (with the wings stretched position), while the "djala uras only ± 60 m long. The "djala uras" cons of a conical shaped bag provided with wings, which are commonly called "suku in Muntjar.

Light plays an important role in fisheries at Muntjar, as fish-lures are not u in this area. Several years ago, torches w used to attract the fishes, but they were l replaced by Petromax lamps (kerosene lam A progressive fisherman has once tried to electric light, but his effort failed becaus technical deficiencies.

The method of catching with the "d uras" in Muntjar is as follows. The fish gathered with a light; as soon as it appears there are enough fish the seine is cast and dr in circle around the lamp. When the two w of the "pajang" or "uras" meet each at proa, the net is immediately hauled into the p At the same time the wings are moved up down and the men in the proa produce as m noise as possible by stamping their feet. prevent trouble when the net is to be hau the lamp is taken away before the net encircled it entirely, or before the two w meet in the proa.

When the fish are encircled, they frightened by the up and down movements of wings, which prevents them from escap in the direction of the wings. The noise in proa deters the fish from approaching it, so the only escape from the encircling ne through the opening of the bag. In this way fish are captured in the bag of the net. process is hastened by pulling the bag tow the proa. All things considered, it looks a everything has been so well planned tha escape could be possible. But in fact this is true, for the batch is rarely proportional to size of the fish shoal.

* Chief, Biological Station, Sea Fisheries Service, Probolinggo, East Java, Indonesia.

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It is very interesting and remarkable that ethod which has been so carefully calculated, fails to give the expected results. It some- s even happens, that the bag is entirely ty, despite the fish having been driven into encircling net. This poses several questions he behaviour of the fish in the net.

FISH BEHAVIOUR WITH RESPECT TO LIGHT

It is clear that these fish can be attracted amp-light. The brighter the lamp, the ter the quantity of fish, presumably because brighter the lamp, the farther the light can ate to all directions and the greater the ber of fish that fall within its influence.

At the time the fishes are centered around lamp, only a small part of the shoal is found e surface, so that the fish are visible from proa, situated at quite a distance from the (10-15 m). At that time fish are jumping of the water near the lamp. A great part of fish shoal is found beneath the surface at the t of illumination and with the reduction of light, the fish will be found to be progres- ly less dense. It might be concluded, that ne light were restricted to a certain small , the fish shoal would be concentrated at place, and could be kept away from the gs of the "djala uras"

4. FISH BEHAVIOUR WITH RESPECT TO OBJECTS

If the fish near the lamp are approached small proa, they disappear from the surface can be found at about 3-5 m beneath the ace of the water. There is a possibility at the time the fish that had been at the ace move to a lower layer, the fish there will move to still deeper layers. So, it might be possible that the movements at the wings of the net will achieve the expected result. But how much influence the moving wings have, is not definitely known. It is also not clear, whether the casting of the net into the water has any influence with respect the fishes. It has also still to be proved, or a more serious study should be made, to know whether the same influence will be obtained if the opening of the bag is quickly pulled towards the fishes.

5. FISH BEHAVIOUR WITH RESPECT TO SOUND

During fishing experiments in Muntjar, observations have been made on fish-behaviour with respect to the sound of the boat-engine. When the boat-engine is suddenly started, the fish gathered around the lamp disappear at once from the surface into the depth of the water for quite a long time. An attempt to catch the fish at that time, would give no result. If the engine is not turned off at the time the fishes are driven to the vessel, the fishes will gradually become used to the sound and will gather again near the lamp. Even when the boat starts to move, the fish will not fly and might be caught.

When people are making a noise in the proa whilst fishing with the "djala ura" the noise may frighten the fish but it is not clear how or in which direction the fish escape in their fright; it is not known whether their escape movement is horizontally or vertically. It is clear that fish that have already been encircled with the "djala ura", disappear from the surface and fly into the circle when frightened and forced to enter the bag, but we also know that the greatest part of the shoal does not enter the bag after all.

4.14 Some Knowledge on Behaviour of Fish Schools

M. Nomura*

0. INTRODUCTION

There is a view among fisheries scientists schooling fish behave differently according he intensity of under-water illumination. Fishermen have long known from experience that fish schools are most active at twilight, in the morning and evening, and hence certain types of gear are operated only during twilight. For some species fished by gill nets, for example,

okai Regional Fisheries Research Laboratory, Tokyo, Japan.

. *Indo-Pacific Fish. Coun.*, (III); 95-96, 1958.

evidence emphatically points to a relation between the age of the moon and the amount of catch.

By using the fish finder recently introduced to scientific surveys, it has become possible to trace the behaviour of fish schools at sea for a length of time.

1. UNDERWATER ILLUMINATION AND SCHOOLING PATTERNS

The pattern formed by schools of sardine *(Sardinops melanosticta)* deduced from fish finder records indicates a peculiar arrangement in which they are found dotted here and there at a depth below the surface during the day, rising to the surface in a group at twilight, then sinking and dispersing at night. Off Yamaguchi Prefecture, in the western part of the Japan Sea, experiments were conducted to observe how the swimming layer of sardine schools would be affected by the intensity of underwater illumination in winter. From the results it is obvious that the fish, having stayed at layers of forty meters or deeper at night, rise all at once to the surface just before sunrise when the underwater illumination in the swimming layers of the schools becomes 10^{-1} to 10^{-2} lux. After sunrise, however, they again submerge to layers deeper than thirty meters, dispersing over the area. Later they tend to sink to a greater depth with increasing underwater illumination. Thus, most of the schools are found in daytime at a range of depths where the underwater illumination is between 10 to 10^{3} lux, although these activities are not so distinct in cloudy weather as on a fine day. With this fact in mind the majority of fishermen of Yamaguchi Prefecture now operate gill nets during the day because with the fish finder they can detect the schools sinking down in such a fashion.

According to a report based on research employing fish finders, the sardine off Ishikawa Prefecture on the Japan Sea coast in April and May begin to form rather small schools towards evening. About one hour after sunset their density increases until at last they throng to the surface at about 20.00-22.00 o'clock, probably for spawning. Later, the fish schools gradually sink down and disperse. Certain exceptions being admitted, such behaviour of sardine schools as described above may be regarded as show some correlation with the general degree underwater illumination although it is lik that there are some differences in the behavi dependent on geographic location, seas oceanographical factors, physiological condit of fish and so forth.

According to information received fr Z. Nakai, who had studied the sardine resour off Korea for years before the War when a la sardine fishery prospered there, tremend schools of the fish usually came to the surf during surveys on research boats or from airplane "spotting" the schools. Very of these fish could be caught by angling from deck. In prewar days, during the sard spawning season in waters off Satsu'nan Reg at the southern tip of Kyushu, every now and t during the survey cruises the sardine sch were observed to come up and swim at surface in the daytime of February and Marc

2. REACTION TO UNDERWATER OBJECTS

Results of a tank experiment show t fish assembled near a black object on a wh background, perhaps receiving a stimulus fr it, or treating it as an escape passage when sca by some other stimuli. In addition, they peared to distinguish to some extent differen in the illumination in surroundings of low li intensity. In association with this fact it interesting to note another experiment mad sea with sardine drift nets. The net used the experiment consisted of square pieces webbing, each with a degree of contrast aga the background different from the adjac pieces joined to it. The results obtained indic that a better catch can be expected from darker than from the lighter ones.

On another occasion, the reaction sardine schools approaching a drift net observed through a fish finder, tracing the m ments they took before and after shooting net. The results indicate that the schools s down when they approach the net, perh heading downward to seek for darker surrou ings. For this reason the fishermen in Ya guchi Prefecture usually set their nets de than the depth of the school they detected.

4.2 Implications for Management

4.21 The Commercial Value of Studies on Fish Behaviour with Particular Reference to Lake Victoria

R. S. A. Beauchamp *

0. INTRODUCTION

Though it may not be necessary for ...rmen to have a detailed knowledge of the ...aviour of fish it is likely that the more they ...w about the habits of the fish they are ...ting the more successful they will be. To ...ease the efficiency of fishermen is not, how-..., the sole reason for undertaking studies ...behaviour.

Such studies are carried out by Research ...cers who are seeking information which will ...ble them to give sound advice concerning ...proper management of the particular fishery ...n which they are concerned. In all cases ...aim must be to utilise existing stocks of fish ...iently and economically without waste. ...quate numbers of fish must be left to breed ... young fish must be allowed to grow to a ...mercially valuable size.

Fishery management based on information ...ved only from statistical analyses of catch ...rds is likely to give rise to restrictive ...slation and the need for such legislation may ... become apparent after the stocks have been ...ously depleted. On the other hand, it can ...shown that such analyses, backed by know-...ge of the behaviour of the fish, can lead to ... framing of more enlightened and often less ...rictive legislation. Moreover, in some cases ...wledge of the habits of the fish may make it ...sible to introduce control measures at an early ...e and so forestall the need for drastic restric-...ns later on.

The development of a fishery is too often ...en as meaning its further exploitation without ...quate compensatory measures to maintain the ...ks of fish. Research should aim at something ...er and it can be shown that knowledge of the ...its of the fish may make it possible to devise ...sures to increase the stocks of fish and so ...elop the fishery in the true sense.

In support of the above remarks on the value of behaviour studies, some notes on the habits of fish in Lake Victoria are appended.

1. TILAPIA

In Lake Victoria, particularly along certain coastlines, suitable spawning grounds for *Tilapia* are limited in extent owing to the growth of papyrus over the littoral. The areas in which *Tilapia* breeds have moderately firm substrate, suitable for nest building. The males build the nests and remain for several weeks guarding them and attracting females to spawn in them. Females usually come to the actual spawing grounds only when fully ripe and leave soon afterwards with the fertilised eggs in their mouths.

Fishing over the spawning grounds leads to the capture of a high proportion of males and to the destruction of ripe females and females carrying entire batches of fertilised eggs. While it is impracticable to prohibit gillnetting over the spawning grounds it is clear that seine netting over these grounds should be discouraged, because not only are breeding fish captured but the substrate essential for nest building may be damaged and existing nests destroyed.

It is natural for fishermen to wish to use seine nets, yet in many areas of the lake the only coastal areas sufficiently free from vegetation for seine netting, are those used by *Tilapia* for spawning. There is therefore unequivocal evidence for restricting the use of seine nets in those areas where *Tilapia* are predominant. (There are, of course, other areas along the more exposed coastlines where fish other than *Tilapia* are more numerous and where the use of seine nets is at present allowed.)

Female *T. esculenta* after spawning retire with their broods of eggs and fry to areas in the lake where there is sheltering vegetation. The

* East African Fisheries Research Organisation, JINJA, UGANDA.

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young are later released in these areas and move out into more open water where gill nets can be set only when they have reached a length of ten or more centimeters. Knowledge of this behaviour made it possible to recommend the use of gill nets of less than three inch mesh for the capture of other species of fish occurring in the area even though *Tilapia* are the most important element in the fishery. This concession was a significant contribution to a policy designed to make the best use of the various populations of fish in Lake Victoria.

In the early days legislation was introduced prohibiting the use of all gill nets with mesh of less than five inches. Thus it can be seen that knowledge of fish behaviour may allow restrictive legislation to be partially relaxed. The fishermen in Lake Victoria, however, make little use of this concession, as they prefer to fish for the larger and commercially more valuable *Tilapia*.

Arising from work done on the breeding behaviour of *Tilapia*, it became evident that an important factor in determining the supply of recruits to the exploited stocks is a shortage of suitable spawning sites. Experiments were therefore carried out to test the value of breeding numbers of *Tilapia* fry of various species in ponds and liberating them in the lake. It was found that these introduced fry grow well and could form a significant addition to the natural stocks. Furthermore, work on the feeding habits of various species of *Tilapia* led to the discovery that *Tilapia zillii* (a species which does not occur in Lake Victoria) eats rooted vegetation, unlike the indigenous species which feed largely on phytoplankton. There is an abundance of aquatic vegetation suitable for *T. zillii* in Lake Victoria and large numbers of these fish have been introduced and are beginning to establish themselves in a number of areas. It is now generally agreed that a policy of restocking the lake from specially built breeding ponds is worth while. Such positive remedial measures designed to offset the declining numbers of fish could not have been instituted without studies on behaviour.

The statistical analysis of records of fish caught may in turn provide information on fish behaviour. It was found that fleets of gill nets of varying mesh sizes fished regularly in particular areas caught progressively fewer *Tilapia*. It was noted, however, that the rate of deci was least in the nets with the largest mesh us namely the five inch net. It was possible deduce from this that whereas the younger tend to remain in the neighbourhood of the a in which they were bred, the older fish becc nomadic and move around from one area another. This opinion has to some extent b confirmed by experiments with marked fish. would seem that the general dispersal of *Til* within the lake and natural restocking of ar where fishing has been intense may depend the migrations of these larger fish. If large survived in numbers below a certain level (to be determined) the *Tilapia* in Lake Victo would most probably be reduced to discrete lo lised populations.

2. CLARIAS

Clarias mossambicus lives in both o water and in deoxygenated swamps. W living in water containing no dissolved oxy it breathes by means of its supra-branchial org However, the eggs and very young fish surv only in highly oxygenated water.

The abundance of this species appear be closely related to the availability of suita inflows in which they can spawn. The sex cycle of this fish is well adapted to make g use of such opportunities as do arise. W the adults are living in the lakes or coa swamps they remain in a state of sexual readin for months at a time. When in this condit the ova are not ovulated and it is not possible fertilise them artificially. However, as soon rain falls and these fish are given the oppor nity to run up a stream, ovulation occurs wit a matter of an hour or so. Under suita conditions of temperature and oxygen tens the fertilised eggs may develop and hatch in little as twenty-four hours. This remarka rapid rate of development can naturally t place only in very well aerated water. Howe after three or four days this high rate of meta lism slows down and the young larvae deve accessory air-breathing organs. (These different from the supra-branchial organ of fully grown fish). The young larvae, once t have reached this stage, can survive in poo oxygenated water.

These reproductive arrangements al these fish to breed successfully in torrents wh

for only a few days at a time. When one biders the natural hazards that these fish t overcome, it is regrettable to have to record the local inhabitants, who are aware of the its of these fish, and of course are able to ge when migration is to take place, place a ety of additional obstacles across the course ne migration.

In anticipation of this run of fish, fences traps made of reeds are constructed in the er courses and as soon as the run begins all local population tramp through the moving er spearing the fish. It was surprising to that many of these people were totally un- re of the significance of this run.

There is little doubt that the numbers of *rias* in Lake Victoria could be significantly reased if the Africans could be persuaded to st from capturing these fish along the course of their migration to the spawning grounds, and until in fact spawning is complete. The traps could quite easily be modified so that the fish could travel up stream yet be caught on their return.

The mouths of the streams down which these spates run and enter the lake are usually blocked with papyrus and other swamp vegetation, so that it is often impossible for the fish to find their way into the stream. It would be to the fishermen's benefit if the mouths of these small streams were kept clear.

Although there is ample food for *Clarias* in Lake Victoria the wholesale destruction of spawning fish prevents the population from growing to a size to make full use of this food. obviously, therefore, the fishery for *Clarias* could be improved if measures were taken to protect the spawning of these fish.

5. CONCLUSION

The results of this Symposium may be summarised as follows:

I. In answer to the question of why fishery biologists should study fish behaviour it can be said that there are many situations in which it appears probable that possession of better information on fish behaviour could lead to improvements in the industry. These situations have been considered in two principal classes: those of fish-searching and of fishing *sensu stricto*, and those of management (in broadest sense) of the industry.

With regard to fish-searching and fishing, it is shown that the presence of fish of a particular species in particular places at particular times is itself an expression of behaviour largely determined by the internal drives of the organism and by its reactions to environmental conditions and to particular environmental directives. Identification of these determinants, and measurement of relations between them and various manifestations of behaviour can furnish fishermen with means of increasing the efficiency of their fish searching.

In this field also the activity of fish on fishing grounds, and their reactions to various natural and artificial elements of the environment are taken into account in design and operation of fishing gear. In many cases these relations are only imperfectly understood so that equipment is used with low degree of efficiency.

With regard to management of fisheries it is obvious that in many respects the magnitude and composition of fish populations is influenced by factors that can modify or interfere with patterns of behaviour. It is not so clear however, in the present state of our knowledge of dynamics of fish populations, considering the assumptions that must be made and the order of accuracy within which calculations are made, that improved knowledge of fish behaviour could lead to a refinement of the results obtained in this field. On the other hand, it is unquestionable that a study of the general biology of any species that neglected behaviour would lack conclusions on many matters. A point that needs to be made here is that although laborious work to measure differentials of behaviour, resulting from fluctuations in determinants, might not be justifiable considering the small improvements such work could bring to equations in population dynamics, qualitative work to ascertain the general features of the behaviour of a species is indispensible to the basic account of its biology.

Whilst the foregoing observations valid for fish of both marine and freshwat they are less relevant to the latter than to former. For freshwater species a knowledge behaviour is likely to be of value to those r ponsible for management who seek to prot fish against harmful effects of man's activit and to take advantage of opportunities cultivate fish stocks in natural and man-ma situations. Behaviour studies can give guidan on action to be taken when spawning migrati are threatened, or actually barred by dams other constructions; similarly, if spawning si are spoiled by pollution, or if a species will reproduce under the conditions offered in pon behaviour research may show how remedial developmental action may be taken.

II. Behaviour research, like other lines scientific enquiry, can be carried out in vari ways. Its programme can be made exceedin complex and can be extended far into physio gical, anatomical and other means of studyi the bases to behaviour. Obviously, as indica in early sections, there are aspects of behavio on which some conclusions can be dra without new research in physiology and rela fields. And even if it should seem likely t results from study of underlying mechanis might call for some revision of conclusi concerning phenomena at behaviour level det mination can be made of the reliance that can placed in behaviour conclusions based assumptions concerning the underlying mec nisms. This is perhaps a complex way of say that useful results can be obtained from stu of more superficial aspects of behaviour. But has also to be said that there are many featu of fish behaviour that can be studied with expensive equipment or large numbers research workers—an aspect that is of con derable importance for countries that as yet ha few fishery research workers and inadequa facilities. In such countries considerable p gress can be made in the study of such matt as distribution, migratory and schooling habi reaction to fishing gear, by participation commercial fishing and analysis of data deriv from them. It would seem that for various reas many of the countries of the Indo-Pacific wou do well to give priority to behaviour research the field, and to contemplate aquarium a laboratory research as a later stage, to be plann on the basis of results from field work.

GLOSSARY

This glossary presents definitions of some the most important terms in common use ong those engaged in behaviour research. In eral it does not include the terminoloy of physiological and anatomical bases to aviour, nor to the circumstances in which anisms find themselves and from which ernal stimuli come, nor to ecological aspects ch as distribution) of which behaviour is a e part.

limation: Physiological adjustment and adaptation of an individual to particular physical and chemical circumstances of an experimental set-up, e.g. in an aquarium.

limization: "The process of habituating, or being habituated, to a new climate". S.O.E.D.

ion-specific energy: (See specific action potential).

aptation: "The process of modifying so as to suit new conditions". S.O.E.D.

erence: "The sum total of all impulses produced by stimuli in any receptor."

Eibl-Eibesfeldt and Kramer 1958.

gregation: "A whole, a mass, formed by aggregating items".

(Aggregate: to gather together into one whole; to mass) S.O.E.D. "of fishes: a local concentration of several separate schools, composed of fishes of one or more species and of different sizes; a temporary formation, heterogeneous and unstable in regard to its specific—and size—composition". (Zusser, 1960 quoting Messyazev).

mental migration: Migration in search of food.

phidromous: "Diadromous fishes whose migration from freshwater to the sea, or vice-versa, is not for the purpose of breeding, but occurs regularly at some other definite stage of the life-cycle". (Myers, 1949.)

adromous: "Diadromous fishes which spend most of their lives in the sea and migrate to fresh water to breed". (Myers, 1949)

Apetitive behaviour: "The locomotor activity characteristics of the organism in which an appropriate internal state (hunger, sexual maturity) has developed and exists in the absence of the environmental releaser (food, a mate)" (Hoar, 1958)

"searching behaviour by which the animal finds the corresponding releasing or satisfying situation". (Raerends 1957)

"it is characterised by (1) its variability and plasticity and (2) its purposiveness."

Eibl-Eibesfeldt and Kramer 1958: "Active seeking, by an animal in a state of special readiness to perform a specific activity, of a stimulus situation which will permit performance of this behaviour." Attribute this term to Craig 1918. See also Van Iersel 1953 and Roeder 1955.

Associative learning: Learning, by an individual, that results from associating, by experience, certain effects with certain actions the individual has taken in response to certain stimuli. Includes conditioning and trial-and-error learning.

Auslöser: (see Social Releasers)

Bathydromous: "Fishes which migrate to deeper water". (Myer, 1949).

Behaviour: "The total of movements made by the intact animal" (Tinbergen, 1951).

"1. Manner of conducting oneself; bearing, manners.

2. Conduct; course of action towards or to others.

3. Handling, disposition of (anything); bearing (of body)." S.O.E.D.

Behaviour pattern: Set of actions following a sequence from an initiating stimulus to an ultimate or consummatory act.

"Innate, stereotyped movements performed under certain conditions by all members of the species in essentially the same way." (Hoar, 1958)

Bewegungsnorm: Muscle activity with fixed coordination for the release of maintenance of which an external stimulus is necessary; the intensity of which is influenced by the strength of the stimulus influences, but whose form is in no way affected by them". (Baerends, 1957, Lorenz, 1957).

Biological threshold: The lowest level of a stimulus to which an organism responds in natural conditions.

Bracheadromous: "Fishes which migrate to shallower water". (Myers, 1949).

Chain Reflex: Passage of a wave or reaction along part of the whole of the body of an organism as a result of the response of one part (body segment) stimulating the response of the part adjacent to it.

Chemical Sense: Perception of chemical substances.

Chemoreceptor: Nerve end organ capable of being stimulated by chemical substances.

Chemotaxis: Action orienting an organism to chemical characteristics of its environment.

Conative behaviour: Behaviour activated by volition and desire.

Conditioned reflex: "If two stimuli S1 and S2 are applied in overlapping sequence, the stimulus S1 being antecedent, then with repetition of such a combination, a plastic change in the nervous system is formed, consisting in the stimulus S1 acquiring the ability to elicit the response of the same kind as the stimulus S2". (Thorpe, 1956)

Conditioned responses: A response, originally an inborn or habitual response to a reward or punishment, given to a new stimulus.

Conditioning: The process of acquisition by an animal of the capacity to respond to a given stimulus with the reflex action proper to another stimulus (the reinforcement) when the two stimuli are applied concurrently for a number of times. (see Thorpe 1956).

Configurational sign pattern: Arrangement elements in the perceptual field, in spa and in time, of a kind that the wh serves as a releasing situation. (s Tinbergen 1952)

Conditioned responses: A response, originally inborn or habitual response to a reward punishment, given to a new stimulus.

Conditioning: The process of acquisition by animal of the capacity to respond to given stimulus with the reflex action prop another stimulus (the reinforcement) wh the two stimuli are applied concurrent for a number of tiies. (see Thorpe 195

Consummatory action: Elements of behavio which, as end-responses, consume t specific impulses responsible for th activation. (Tinbergen, 1951, Lorenz, 19 Craig, 1918).

Cruising speed: "That speed at which the fi could swim steadily for some considera period of time". (Fry and Hart, 1948).

Diadromous: "Truly migratory fishes whi migrate between the sea and fresh wate (Myers, 1949)

Directive factor: (Fry, 1947)

Displacement Activity: "The performance of behaviour pattern, usually in an incomple eccentric, or imperfectly oriented for out of the functional context of apetiti and behaviour patterns to which it normally related, as a consequence tension and the resultant deflexion energy." (Armstrong, 1950)

Dorsal light reaction: An orientation moveme in which the animal does not move towa the light but at right angles to i (Fraenkel and Gunn), but Tinberg (1951) considers this to be an orient movement as a whole (taxis-fixed patte combination) confused with a pure tax component.

Drive: "The complex of internal and extern states and stimuli leading to a giv behaviour". (Thorpe, 1951, 93:1-52 a 252-296) (Baerends, 1957).

logenous rhythm: Regulated succession of strong and weak values of some characteristic of an organism, of which the variation has its origin in the physiology of the organism.

kkoordination: Syn. for Fixed (action) pattern.

otogy: The objective study of behaviour.

genous rhythms: Regulated succession of strong and weak values of some characteristics of an organism, of which the variation is induced by forces external to the organism.

loratory behaviour: (see also Appetitive Behaviour)

loratory movement: Movement of an organism to investigate its surroundings.

ed pattern: "An integration of muscle contractions controlled from within" (Tinbergen, 1951)

"An invariable pattern of muscle activity on which is superimposed another pattern, variable in relation to external stimulation".

Baerends, 1957, citing Lorenz.

ght reaction: Movement by an organism to escape from inimical forces.

vanotaxis: Orientation to electrical current.

vanotropism: (see Galvanotaxis).

tropism: Orientation to the gravitational field.

talt: Form. (The gestalt school considered placed considerable emphasis on the significance of the perception of things and situations as wholes, with appreciation of relations).

nituation: "An activity of the central nervous system whereby innate responses to certain relatively simple stimuli, especially those of potential value as warning of danger, wane as the stimuli continue for a long period without unfavourable results". (Thorpe, 1950)

"The relatively permanent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement." (Thorpe, 1956)

Hierarchical organization: Arrangement of mechanisms underlying reactions in a system of various levels of integration at each of which an external stimulus can have a specific releasing influence, and each reaction has its own motor pattern. (see Tinbergen, 1952)

Heterogeneous summation: "Different elements which go to make up a total inherited releasing pattern can cat separately, but can also summate to give steadily increasing stimulation as more and more elements are added" (Seitz, 1940, cited by Thorpe, 1956).

Innate behaviour: "Behaviour that has not been changed by learning processes". (Tinbergen, 1952)

Innate releasing mechanism: "A special neuro—sensory mechanism that releases a reaction and is responsible for its selective susceptibility to such a very special combination of sign stimuli" (Tinbergen, 1951).

Insight: "The apprehension of relations" (Thorpe, 1950)

Insight learning: "The sudden adaptive reorganization of experience or the sudden production of a new adaptive response not arrived at by random trial behaviour". (Thorpe, 1950)

Instinct: An innate propensity of organisms to perform certain acts.

Instinctive activity: Combination of fixed pattern and taxis. Baerends, 1957. Named by Lorens, 1937 (syn. instinctive movement. Instinkthandlung, Instinktbewegung).

Eibl—Eibesfeldt and Kramer 1958: Refer to this as 'instinctive act' and say that it may include appetitive behaviour and releaser mechanisms as well as a taxis and instinctive movements.

Instinkthandlung: Syn.: instinctive activity (act)

Instinctive movement: (see instinctive activity).

Instinkt—Taxis Verachränkung: (see Instinctive activity).

Intensity optimum: The level of intensity of an environmental force to which an organism gives a response that is best from some viewpoint or other.

Intensity preferendum: The level of intensity, of a gradient of some environmental force, that an organism wil seek.

Internal motivation: "The state of the animal responsible for its readiness to perform the behaviour pattern of one instinct in preference to all other behaviour pattersn" (Thorpe, 1951); "a common internal factor causing a grouping of activities in an ierarchical organization". (Baerends 1957).

Klino taxis: Orientation, independent of the actual direction of the source of the stimulus, but dependent no the different intensities of two stimuli administered in succession. (from Tinbergen, 1951)

Learning: "A process leading to the lasting changes in the manner in which an organism reacts to a stimulus which are due to the application of this stimulus in definite combinations with other stimuli, and which are not caused by any destructive effects which the applied stimulus might produce." (Konorski, 1950)

"That process which manifests itself by adaptive change in individual behaviour as the result of experience." Thorpe, 1956.

Leerlaufreaktion: (see vacuum reaction). "The damming-up of reaction-specific energy' so that the 'instinctive act' goes off *in vacuo* completely independent of the animal's receptors". (Lorenz, 1939, fide Armstrong, 1950).

Maintenance Activity: Action by an organism to meet its needs of food, shelter, protection from enemies and so on. (see Russel, 1958).

Menotaxis: "Light compass reaction" (a special case of telotaxis: Tinbergen 1951)

Mnemotaxis: Kühn: orientation dependent on a number of landmarks and involving memory (from Tinbergen, 1951) and rejected by Tinbergen as concerning the developmental history of the taxis, not its mechanisms.

Mutualism: "Symbiosis is often defined to include only mutually beneficial relations of such partners..... The term 'mutualism'... corresponds to/this/more limited concept of symbiosis." (de Bary 1879)

Orientation to Currents: To tides, to light.

Orienting factor: (Baerends, 1957).

Orthokinesis: "Undirected movement of whi the speed is correlated with the strengt the stimulus". (Carthy, 1958 from Fraen and Gunn, 1940)

Orthotaxis: Directed movement of which t speed is correlated with the strength of t stimulus.

Overflow activity: "Behaviour impelled by powerful a drive that it finds expressi even when the stimulus from the percept field is suboptimal or minimal". (Ar strong, 1650)

Partial reflex: "The 'automatic response o single organ or organ system to a sim response'" (Thorpe, 1950)

Phototaxis: "Trial-and-error orientatio (Kuhn, 1919, vide Tinbergen 1951) Oriented reaction to light stimulus.

Photokinesis: Kinetic reaction to light stimul

Phototropism: (See phototaxis)

Physiological threshold: The level of intensi of a stimulus to which an organis responds, as measured by physiologic techniques.

Plastic changes: Those lasting changes produc in the manner in which an organism rea to a stimulus which are led to by learni (Konorski, 1950) para

Random Movement: (see also Appetiti Behaviour)

Reaction Chain: "A series of separate reactio each of which is dependent on a spec set of sign stimuli, which occur in special set of sign stimuli, which occur a sequence to appear as a single reactio (See Tinbergen, 1952)

Reactive behaviour: Behaviour "dependent external stimulation" (Tinbergen, 1951

Reaktionsnorm: Muscle activity in which coor nation is less rigid, and in which adapti changes corresponding to properties of t stimuls are possible in accordance wi fixed rules." Baerends, 1957, Lorenz, 19

ex : Passage of a nerve impulse, initiated by stimulation of a receptor, to the central nervous system, outwards to an effect or element.

ex arc : The nervous pathway, consisting of receptor, sensory neurone, elements of the central nervous system, and motor neurones, along which nerve impulses pass in a reflex.

roductive behaviour : Activity of an organism leading to reproduction.

-o- kinesis : Kinetic reaction to current.

otaxis : Orientation to current.

otropism : See rheotaxis

ool : (fish) : " An aggregate formed when one fish reacts to one or more other fish by staying near them " (" the chief factor common to all schools is a definite mutual attraction between individuals ") (Keenleyside, 1955)

ooling : Fromation a school by fish of a single spacies and sometimes of a particular size-composition.

king Behaviour : (see also Appetitive Behaviour)

n stimuli : The particular stimuli of the environment that lead to the release of specific innate behaviour actions.

al releasers : Releasing mechanisms specialised to respond to stimuli produced by one animal and influencing another and evoking a special kind of behaviour. (from Baerends, 1957).

cific action potentiality : (S.A.P.) " That state of the animal responsible for its readiness to perform the behaviour patterns of one instinct in preference to all other behaviour patterns " (Baerends, 1957, citing Thorpe 1951, Hinde, (1954)

cific exhaustibility : " The ' draining-off ' of ' reaction - specific energy ' " (Lorenz, 1939 *fied* Armstrong, 1950)

Spontaneous behaviour : Behaviour " independent of external stimulation, but dependent on internal causal factors, or motivational factors, responsible for activation of an urge or drive " (Tinbergen, 1951)

Stimulus : " Any compound of agents acting on the receptive parts of the nervous system (i.e. on receptors, afferent pathways, or directly on nervous centres) and evoking their excitation " (Konorski, 1950)

Substitute Activity : See ' Displacement Activity '

Symbiosis : " Includes... commensalism in which the benefit relation is onesided, without injury to the host, and parasitism, in which the relation is typically detrimental to the host. The term ' mutualism '...corresponds to the more limited concept of symbiosis... " (De Bary, 1879)

Taxis : " An integration of reflex - like reactions, responsible for orientation ". (Tinbergen, 1951)

Telotaxis : Orientation enabling an organism to pursue a straight path toward a stimulus source. (from Tinbergen, 1951)

Thermotaxis : Orientation to heat gradient,

Topotaxis : " Oriented movement " (Kuhn, 1919. vide Tinbergen, 1951)

Trial and error : (see also Phobotaxis)

Tropism : Equals tropotaxis, Tinbergen 1951. The term is Loeb's.

Tropotaxis : Movement directed by a simultaneous comparison of intensities of the stimuli acting upon two receptors or upon two parts of one recepor. (from Tinbergen, 1951)

Vacoum activity : (see Leerlaufaktion) " An activity performed, not released for a very long time, without any of the adequate releasing stimuli being present ". (Baerends, 1957)

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